SOME TERTIARY AND RECENT CONESCHARELLINIFORM BRYOZOA

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CONTENTS

SYNOPSIS

The characters of conescharelliniform and orbituliporiform colonies of Bryozoa, and the occurrence in both groups of two types of astogeny, 'normal' and 'frontal', are described. The genera *Conescharellina* and *Trochosodon* are known to be anchored to their substrata by rootlets. They are compared with the genera *Batopora*, *Lacrimula* and *Atactoporidra*. A hypothetical model for the primary colony development of these genera is suggested. The characters and distribution in time and space of the genera *Batopora*, *Lacrimula*, *Atactoporidra* and *Conescharellina* are discussed, and the available information on their ecology and palaeoecology is

recorded. Full descriptions are given of three species of *Batopora*, two of which are considered to be new, and of seven species of *Lacrimula*, four of which are considered to be new. The combined effects of genetics and environment outweigh microenvironmental influences within the colony. Integration within colonies is considerable, and is demonstrated by the interzooidal communications, astogenetic zonation and polymorphism. The specialized mode of life allows palaeoecological inferences to be made as to depth and type of sea-bottom from the Eocene to the Recent.

INTRODUCTION

MARINE cheilostomatous Bryozoa have evolved colony forms capable of inhabiting many environments. Members of the ascophoran families Orbituliporidae and Conescharellinidae particularly appear to be adapted to conditions unsuitable for many other forms. The members of the two families are closely similar in many characters, not least in the possession of a form of astogeny which may be unique among Bryozoa (see below). Both families exhibit parallel groups of genera with distinct colony forms, and it must be stressed that those which are here considered to be 'orbituliporiform' colonies are found both in the Orbituliporidae (e.g. some species of *Orbitulipora*) and in the Conescharellinidae (e.g. *Flabellopora*). Conversely, 'conescharelliniform' genera are found in the Conescharellinidae (e.g. *Conescharellina*) and in the Orbituliporidae (e.g. *Batopora*). Other genera exhibiting similar colony forms have no close systematic relationship with these families and have an entirely different astogeny (see below). For example, 'orbituliporiform' colonies occur in *Lanceopora* and 'conescharelliniform' colonies in *Fedora*.

This paper is principally concerned with the colony structure, diversity, distribution and relationships of three conescharelliniform genera, *Batopora* (Eocene to Recent), *Lacrimula* (Eocene to Recent) and *Atactoporidra* (Eocene to Oligocene). The relationships and distribution of a fourth genus-group, comprising some representatives of the genera *Trochosodon* and *Conescharellina*, are briefly compared.

Conescharelliniform colonies are small, rarely reaching 8 mm in height or diameter. They are conical, usually with no large basal concavity, and apparently without substratum. The ancestrula or ancestrular complex is concealed by secondary kenozooidal or extrazooidal tissue in later astogenetic and ontogenetic stages. Orbituliporiform colonies are frequently larger, often reaching 20–30 mm in height or diameter. They are actually or apparently bilaminar, and may be disc-shaped, sagittate or trilobate. One of the disadvantages in defining colony form in terms derived from names of genera which illustrate a distinct type of structure is that the terms themselves may begin to carry with them a systematic connotation. The term 'lunulitiform' (from *Lunulites*) is, however, now generally used for cup-shaped or conical colonies which are free-living, and which at some stage in their astogeny have a basal cavity. Although the overall form of these colonies is similar, the budding pattern, microstructure and interrelationships of polymorphs are totally dissimilar. Unrelated genera included in this grouping are, for example, *Lunulites*, *Cupuladria*, *Selenaria* and *Cyttaridium*.

Conescharelliniform and orbituliporiform colonies have, in common with lunulitiform colonies, an association with fairly calm to calm, often deeper shelf waters, and a soft unstable sea-bottom, with the concomitant problems to the bryozoan of

deposition and restricted availability of substratum for settlement of larvae. Unlike lunulitiform colonies, orbituliporiform and conescharelliniform colonies may inhabit abyssal depths and have been observed, or may be inferred, to possess cuticular rootlets as an essential part of the colony structure.

The astogeny of both types of colony may be similar to that found in encrusting cheilostome species ; i.e. new zooid buds arise from the distal or distal-lateral walls of existing zooids, forming linear series of increasing astogenetic age in the direction leading away from the ancestrular area ('normal astogeny'). In other colonies of both groups new zooids are budded entirely from the frontal walls of existing zooids in a succession which is described in detail below (p. 324) as 'frontal astogeny'. Conescharelliniform and orbituliporiform genera exhibiting these forms of growth include :

Conescharelliniform colonies	'frontal astogeny'	*Conescharellina, Trochosodon, Batopora, Lacrimula, Atactoporidra, Fedorella*
	'normal astogeny'	*Fedora, Kionidella, Mamillopora*
Orbituliporiform colonies	'frontal astogeny'	*Orbitulipora, Flabellopora, Zeuglopora*
	'normal astogeny'	*Lanceopora*

TERMINOLOGY

Classical terms in bryozoan morphology have rather wide definitions, but in practice some have been found to be satisfactory. There are considerable difficulties, however, in applying these terms to the genera discussed here. These stem in part from the peculiar structure of the colonies themselves, and in part from the fact that their orientation in life is unknown.

Distal and basal walls as such do not exist in these colonies, and the classical 'distal' direction of the astogenetic process is apparently 'proximal'. The orientation of the colony in relation to the substratum is not known from direct observation. The term 'distal' usually refers to that direction, and by morphological analogy, to those zooidal walls, and parts of the whole colony, which are astogenetically 'away from' the ancestrular area. Similarly the conventional representation of conical, lunulitiform colonies assumes that the geometric apex of the cone is uppermost, as in these colonies the basal walls are, by direct observation of living forms, directed downwards (see Cook, 1963 ; Greeley, 1967). The terms used here are defined below (see Figs 1 and 2).

Adapical – directed toward the apical region of the colony (the classically 'distal' part of the orifice is adapical).

Antapical – directed away from the apical region of the colony.

Apical region – the region of the colony in which the ancestrula and primary zooids may be observed or inferred to occur.

Concealed frontal wall – that part of the frontal wall of each zooid which, except in the proliferal region, is hidden from view. Primary series of frontal buds originate from this part of the wall.
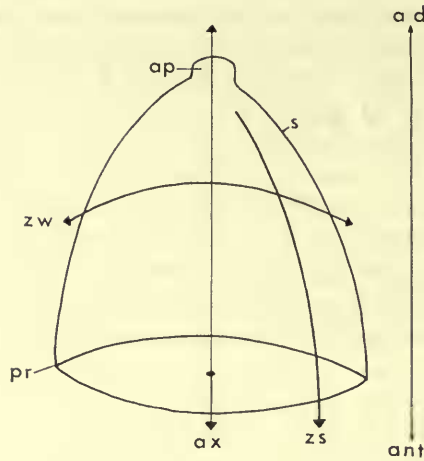
FIG. 1. Terms used in describing conescharelliniform colonies with 'frontal' budding. Note that the colony orientation in life is *not* known. *ad*, adapical direction ; *ant*, antapical direction ; *ap*, apical region ; *ax*, colony axis ; *pr*, proliferal region ; *s*, colony surface ; *zs*, zooid series ; *zw*, zooid whorl.

Exposed frontal wall – that part of the frontal wall of each zooid which surrounds the orifice and which contributes to the exposed surface of the colony between its geometrical apex and its geometrical base.   Secondary series of frontal buds may originate from this part of the wall.

Proliferal region – the region of the colony in which the most recently formed primary zooid buds (i.e. those of the primary zone of astogenetic change) may be observed or inferred to occur.

Rootlets – long cuticular kenozooids or zooidal extensions arising from specific positions in a colony, actually or hypothetically functioning as anchoring structures.

Rootlet pores – small areas, which may be kenozooids derived by frontal budding from frontal septulae, from which rootlets may be observed or be inferred to originate.

  Abbreviations used:

AxL	axial length of colony
Prl	proliferal region width of colony
Lfw	length of exposed frontal wall
lfw	width of exposed frontal wall
Lo	orifice length
lo	orifice width
Lov	ovicell length
lov	ovicell width
Lt	length of apical tube
BM	British Museum (Natural History)
NMV	Naturhistorisches Museum, Vienna
USNM	United States National Museum

STRUCTURE AND BUDDING

Apparent reversal of the orientation of the zooidal orifice occurs in two distinct forms in Bryozoa. In the Inversiulidae the operculum opens in a distal direction, but all other zooidal relationships appear to be normal (see Harmer, 1957 : 956). In the Conescharellinidae and Orbituliporidae the whole zooidal orientation is apparently reversed in relationship to the direction of budding of the colony. The classically 'distal' part of the orifice is thus directed towards and not away from the ancestrular region.

Hypothetical models illustrating the methods involved in this reversal have frequently been made in the past, two of the most recent being those of Silén (1947) and Harmer (1957). They have been based on the assumption that budding in Bryozoa is primarily a function of the distal and/or lateral zooidal body walls. In the Cheilostomata, the astogeny of the great majority of species consists of the production of a primary uncalcified bud by the expansion of cuticle and underlying epidermis distally from an existing zooid. The bud usually proceeds to secrete calcified basal and lateral walls, and becomes limited distally by the growth of a transverse distal wall. Coelomic connection between and among zooids is through septulae in the lateral and distal walls.

Recently, studies have been made on another type of astogenetic series in the Ascophora, the formation of 'frontal' buds (see Banta, 1972). Hastings (1964), in
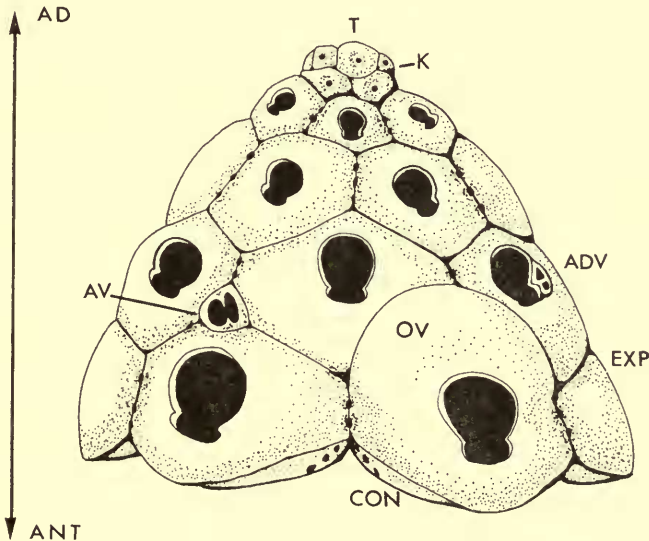
FIG. 2. Generalized morphology of a conescharelliniform colony with one zone of asto-
genetic change. Colony has four zooid whorls and six zooid series budded alternately.
Note condyles of zooid orifices, marginal pores, avicularia and ovicells. AD, adapical
direction ; ANT, antapical direction ; CON, concealed frontal wall ; EXP, exposed frontal
wall ; T, position of internal or external apical tube ; K, apical area of kenozooids, and/or
closed zooids or extrazooidal tissue ; AV, interzooidal avicularium ; ADV, adventitious
avicularium ; OV, ovicell.

describing the colony structure of *Reginella doliaris* (Maplestone), a cribrimorph species with a free-living conical colony form, postulated a kind of frontal budding, and compared the astogeny with that of *Conescharellina*.

Although there may be several methods by which these frontal buds are formed, the sequence of development is basically as follows. There is an expansion of cuticle and underlying epidermis above the calcified frontal wall of an existing zooid. Coelomic connection is provided by frontal septulae, which seem to be represented by some or all of the marginal pores. The buds so produced have no cuticle basally, and some do not appear to have lateral walls. Marginal septulae are present. Some colonies may show long series of frontal buds which develop in a plane at right angles to that of the primary growth (see also Boardman, Cheetham & Cook, 1969, fig. 5). Other colonies may produce small groups of frontal buds, which then proceed to bud distally and laterally, forming a secondary layer of zooids above and parallel to that of the primary growth (similar to an 'overgrowth' of Boardman *et al.*, 1969, fig. 6). Zooids of this kind of secondary layer may therefore be distinguished from frontally budded layers by the possession of a basal wall and basal cuticle.

In the Conescharellinidae and Orbituliporidae normal distal or distal-lateral budding appears to have been completely abandoned in favour of frontal budding. Each zooid may be considered to have a calcified frontal wall which has extended at the expense of the distal, lateral and basal walls. At the same time, the frontal wall has become divided into two elements. The first element is a flat or inflated, often hexagonal portion which represents the projection of the geometrical base of a cone at the surface of the colony. The second portion consists of part of the remainder of the cone. The 'basal' wall of each zooid completes the cone, but this is composed of the frontal wall, or walls, of the parent zooid or zooids (see Figs 2 and 3). Marginal pores, which are inferred to be septulae, are placed round the periphery of the hexagonal portion of the frontal wall and in two converging rows on its remaining surface ('exposed' and 'concealed' frontal wall elements, see p. 321). The next generation of frontal buds is produced either directly from one or from between two existing zooids, arising in a line extending along the 'concealed' part of the frontal wall toward the centre of the colony, and thus including two series of marginal pores. As the bud enlarges it completes the conical shape, and the enlarged frontal wall calcifies, the geometrical base of the zooid cone again forming the hexagonal exposed frontal wall at the surface of the colony, and surrounding a centrally placed orifice.

In both families, buds are produced in direct or in alternating series, i.e. only one, or two to three zooids of the previous generation contribute to the next generation. In the Conescharellinidae the type of budding is usually direct and specific. It was illustrated by Harmer (1957) for most species of *Conescharellina* and *Trochosodon* (but *C. ovalis*, p. 743, buds in alternating series). In the Orbituliporidae, most species bud in alternating series, and there is a good deal of intracolony variation. Even in zooids budded directly, there may be a variable contribution from other zooids, potentially at least, as their marginal pores are incorporated beneath the frontal wall of the new bud. Some colonies, for example the largest of *Lacrimula burrowsi*, show an initial secondary zone of alternating budding, which, as it gives

rise to a few intercalary series of zooids, becomes somewhat irregularly direct at the later astogenetic stages. A few species do appear to be regularly directly budded ; these are *Batopora ernii* as figured by Dartevelle (1948) and *Lacrimula visakhensis*. *Batopora murrayi* also has strong tendencies to directly budded series of zooids. The very regularly directed budded zooids figured by Reuss (1867), in *Batopora rosula* are not in fact of this type (see p. 351).

If the first circle of buds is regarded as consisting of frontally budded zooids from an ancestrular complex (see below), the apparent reversal of normal zooid orientation is explicable. Theoretical explanations of reversal of the operculum and viscera, or of the proportions and roles of the basal, lateral and distal walls (see Harmer, 1957), are not necessary. In other, unrelated genera colonies do exist in which instead of a frontal wall development at the expense of other walls, the frontal wall is very restricted, and the lateral and distal walls greatly increased in extent, as postulated by Harmer (1957) for *Conescharellina*. It is interesting that these colonies have a conical shape, and may have a mode of life similar to that of the frontally budded colonies described here. For example, the lunulitiform genera *Anoteropora* and *Actisecos* are associated with ecological conditions similar to those in which the orbituliporiform and conescharelliniform genera are found.

Conescharelliniform colonies belonging to the Conescharellinidae and Orbituliporidae may be considered to have a primary zone of astogenetic change which never develops into one of astogenetic repetition (see Boardman *et al.*, 1969), because the zooids become progressively larger throughout the budding series. In some forms, such as *Atactoporidra* and some species of *Lacrimula* and *Batopora*, the primary zone may develop almost concurrently with, or be replaced by, a secondary zone of change. This secondary zone comprises a secondary series of buds which are produced from the exposed frontal walls of zooids of the first zone of change (see Fig. 3). In *Atactoporidra*, further series of such frontal buds may eventually form a primary zone of astogenetic repetition.

In the genera studied here, interpretation of colony structure, and even recognition of species, is complicated by the development of secondary and occasionally tertiary zones of change. These may involve part of the colony or the whole colony, and are accompanied by astogenetic and ontogenetic changes in the apical region.

During the course of this work we have been fortunate in having been able to examine several populations which show almost complete astogenetic series. This has not only enabled us to postulate a model for the earliest astogenetic stages, but has made it possible to infer parallel series of changes in less representative or less well-preserved populations.

Secondary, frontally budded zones of change are present in some species of all three genera principally studied. The secondary zone originates adapically in *Lacrimula* and *Batopora multiradiata*, and follows a regular, but entirely different pattern in the two genera. In *Lacrimula* (see Fig. 3B) each apical zooid produces one, or occasionally two, frontal buds directly from its exposed frontal wall. Further secondary zone buds arise in a similar fashion and in a regular sequence in an antapical direction. The adapical zooids frequently have closed orifices at the stage when the secondary buds are produced, but in more antapically placed zooids of the
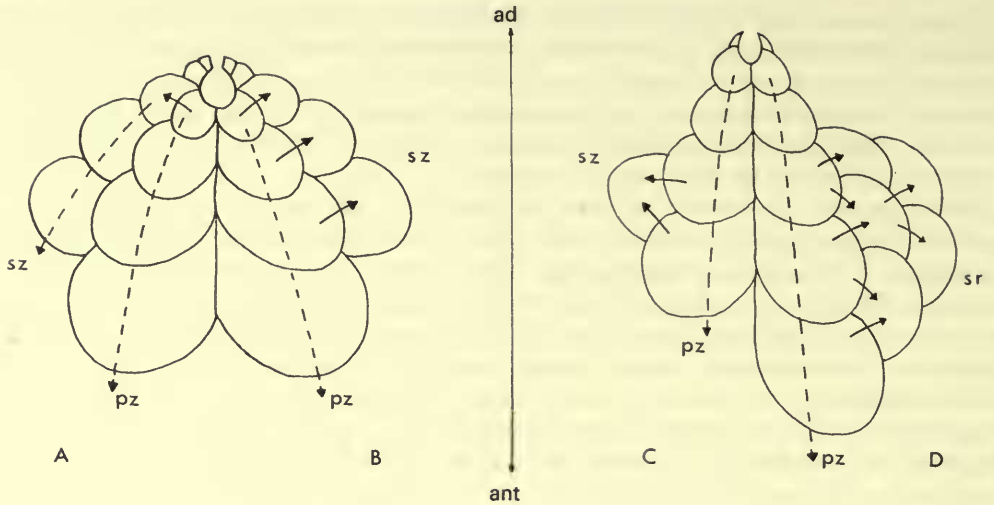
Fig. 3.   Patterns of secondary budding in conescharelliniform colonies with 'frontal'
astogeny.   *pz*, primary zone of astogenetic change ;   *sz*, secondary zone of astogenetic
change ;   *sr*, secondary zone of astogenetic repetition.   *ad*, adapical direction ;   *ant*, antapi-
cal direction.
    A. Primary zone followed by antapically directed overgrowth of frontally budded
secondary zone of change (e.g. *Batopora multiradiata*).   B. Primary zone followed by a
secondary zone of directly frontally budded zooids.   Sequence of budding antapically
directed (e.g. *Lacrimula*).   C. Primary zone followed by isolated interzooidally budded
secondary zooids (e.g. *B. clithridiata*).   D. Primary zone followed by directly or inter-
zooidally budded secondary zooids eventually forming a zone of repetition.   Secondary
buds often arising antapically, and sequence of budding adapically directed (e.g. *Atacto-
poridra*).

primary zone, the orifices are not closed by calcification, and may be seen through
the orifice of the secondary frontal bud.   In *B. multiradiata* (see Fig. 3A) the second-
ary zone arises in the same manner as in *Lacrimula*, as a circle of apical frontal buds.
These zooids then proceed to bud the next generation antapically from their con-
cealed frontal walls.   This secondary zone advances, often very regularly, over the
primary zone zooids.   It is thus an overgrowth, but one which consists of frontally
budded zooids, not those of 'normal' astogeny.

    In all other species of *Batopora* secondary zooids may be produced randomly and
irregularly between primary zooids as interzooidal frontal buds (see Fig. 3C).   In
Atactoporidra, the secondary zone arises antapically, in contrast to *Lacrimula*, and
may extend adapically.   Zooids arise as interzooidal frontal buds and in some
colonies this process is continued through three generations of zooids and results in
a zone of repetition (see Fig. 3D).

    The astogeny of *Conescharellina* is basically of a similar pattern but differs in that
the axial part of the proliferal region is filled with kenozooids, and sometimes
avicularia, budded between zooids from the axial part of the concealed frontal walls.
As the colony increases in size, avicularia and kenozooids arise between zooids along

the whole length of the concealed frontal wall. When colony growth ceases (at various astogenetic stages which may be correlated both specifically and with unknown environmental conditions) the entire antapical area becomes covered by kenozooids and avicularia. These form a secondary zone of astogenetic change and eventually of repetition, but secondary zones of autozooids do not seem to occur in *Conescharellina*. A form of growth somewhat analogous to that of *Atactoporidra* is found in some 'celleporiform' colonies which grow on hydroids. Here the primary zone of change is formed of a small number of zooids encrusting a very restricted substratum. The major part of the colony consists of zooids of a secondary zone of change and repetition formed by frontally budded erect interzooidal zooids.

In orbituliporiform colonies a primary zone of astogenetic repetition is usually established after a variable number of generations. The zooids do not continue to increase in size, but intercalary frontally budded series are produced in both laminae.

Conescharelliform and lunulitiform genera have somewhat similar shapes and it is interesting to compare the role played by zooidal size in colony structure. In lunulitiform colonies, especially those belonging to the Cupuladriidae, which have a triadic ancestrular complex, the conical shape is achieved by the budding of inter-calary rows. After the zone of repetition is established, there is little or no increase in zooid size. Even in *Cupuladria doma*, where the highly conical colony resembles that of *Conescharellina*, and where there is a small but continuous increase in size, a colony which begins with a zooidal triplet will have 30 closed peripheral zooids when it reaches full size (see Cook, 1965, fig. 3). In conescharelliniform colonies, relatively few intercalary series of zooids are produced, the conical shape resulting from a steady increase in size of the zooids of successive whorls. There are, of course, exceptions to this rule (see p. 366).

ORIENTATION OF THE COLONY, ROOTLETS AND EARLY ASTOGENY

The colonies considered here all have structures which have been observed, or may be inferred to have been associated with cuticular rootlets, which served as organs of attachment.

Orientation in life of conical and bilaminar colonies with rootlets has been the subject of a great deal of speculation in the past (see Silén, 1947; Harmer, 1957 : 724–725). It is possible that some colonies may live suspended by rootlets from algal fronds, or from hydroids, worm tubes or other Bryozoa. It is equally possible that they may be supported at or above the surface of a soft and unstable sea-bottom by rootlets which function as an anchor. These alternative theories of mode of life are not mutually exclusive, and the rootlets could perform either function.

Until observations are made upon living colonies, and their larval life and settle-ment preferences are known, discussion of orientation and mode of life must remain purely speculative.

Generally, those rootlets which have been observed have very thin cuticular walls, and may therefore not be comparable in function with those found in the Scrupocellariidae and Petraliellidae, which are strong enough to support the colonies above a substratum. Numbers of thin-walled rootlets would, however, have

sufficient strength to support the smaller orbituliporiform colonies. Colonies of
Flabellopora and *Lanceopora*, which are flattened and sagittate, and may be more than
30 mm in height or diameter, are known to have numerous rootlets which originate
in the ancestrular region, and which are associated with kenozooids and extra-
zooidal tissue. From evidence of adherent Foraminifera and sand grains, these
colonies are inferred to be anchored by their rootlets at the surface of the soft and
unstable sea-bottoms with which they are associated. Many of the stations which
have yielded specimens of these genera have also provided numerous specimens of
Conescharellina (see Canu & Bassler, 1929a ; Silén, 1947 ; Harmer, 1957).

Rootlets have been seen in Recent specimens of *Conescharellina* and the closely
related genus *Trochosodon*. These arise, principally, in the apical region, from
specialized rootlet pores ('lunoecia'), which are apparently modified kenozooids
budded frontally among the autozooids (see Pl. 1, figs 4 and 5), and which them-
selves may bud frontal avicularia (see Harmer, 1957 : 742). Not all forms of
Conescharellina have distinct rootlet pores, however, but have complexes of keno-
zooids in the apical region which may form a solid structure, surrounded by avicularia,
as in *C. africana* (see Cook, 1966), or a distinct tube, as in colonies of an unnamed
species from Zanzibar (see Appendix 3, p. 372). These apical structures are very
similar to those found in *Lacrimula* and some colonies of *Batopora*. The apical
region in *Batopora* has usually been described as a 'pit'. In many colonies, a round
cavity with thick calcified walls is present, surrounded by a circlet of zooids or keno-
zooids. In other colonies the cavity is surrounded by a raised series of kenozooids
forming an external, often elongated tube. The sequence of astogenetic and onto-
genetic changes is not fully known, and may be environmentally influenced, as
different forms of apical structure occur among colonies of similar astogenetic age in
a single population. In *Batopora* and *Lacrimula*, subsequent ontogenetic changes
include a thickening of the calcified walls, and astogenetic changes consist of a
proliferation of frontally budded kenozooids, presumably by adapically directed
growth of units from the exposed frontal walls of the primary kenozooid and zooids.
The kenozooids each have a small uncalcified area, from which it is inferred that
rootlets could originate. In *L. asymmetrica*, the primary kenozooid is itself very
elongated and tubular (see Fig. 6, p. 362). It appears to enlarge and become thicker
walled during colony development, but whether this is an ontogenetic change, an
astogenetic change or a change involving extrazooidal colony-wide calcification is
not known (see Pl. 5, fig. 4). Small uncalcified areas are present upon both the
external and internal surfaces of the tube. In some colonies of *B. rosula*, and in
B. scrobiculata, the tube is apparently formed by a secondarily-budded kenozooid,
which has similar uncalcified areas on its outer walls. In other species of *Lacrimula*,
and in *Atactoporidra bredaniana*, the tube is composed of small kenozooids, which
arise adapically as a regular series from the primary zooids (see Pl. 5). This also
occurs in some colonies of *B. multiradiata*. Other changes in the apical region,
found particularly in *Lacrimula*, include progressive, antapically directed closure
of the orifices of the primary and later-budded zooids. At the same time, the ex-
posed frontal walls of these apical zooids become thickened, perhaps extrazooidally.
Evidence of some developmental sequences has been seen in very young colonies.

In *B. stoliczkai*, *B. murrayi*, *L. asymmetrica* and *Trochosodon* sp. a kenozooid appears to be one of a primary group of zooids. The walls of the kenozooid are calcified, but there is always a large, round, uncalcified area adapically. It is inferred that this marks the position of origin of an uncalcified rooting or anchoring element.

In *L. asymmetrica* the primary complex consists of five zooids and a long, tubular kenozooid (see Fig. 6). One of the five zooids is asymmetrical and may have been developed before the remaining four. If the kenozooid was involved in the growth of a rootlet, it was present from the earliest stage, and remained prominent, becoming larger in subsequent growth stages of the colony (see p. 362). In *B. murrayi* there is a primary pair of zooids, followed by a triad. The exposed frontal walls of the primary pair and two of the subsequent triad surround a large rounded apical cavity which itself has calcified walls. This is inferred to mark the site of an immersed primary kenozooid. In *B. stoliczkai* (see Pl. 1, fig. 1) there is a primary zooid pair and a large kenozooid with a prominent round aperture. Later stages show a 'pit' surrounded by calcification or kenozooids at this point, and it is inferred that the kenozooid is part of the primary group. A young colony of *Trochosodon* sp., a genus known to have rootlets, shows a zooidal triad and a large rounded cavity which is inferred to mark the position of a primary kenozooid. Although this colony comprises only ten zooids, it has secondarily budded apical avicularia and three semilunar rootlet pores. The general similarity of the modes of growth of these colonies is shown in Fig. 6 and on Pl. 1, figs 1–6.

Harmer (1957 : 748, fig. 78) made some interesting observations on the early development of *Trochosodon*. He remarked : 'There is doubtless some variation in the details of the early development.' He concluded that in some specimens of *T. optatus* there was an ancestrula and paired primary zooids. In view of its prominence, it is possible that the 'ancestrula' was an apical kenozooid. The specimen of *T. linearis* figured by Harmer (1957, fig. 75) was drawn from the 'basal' side by transmitted light. In reflected light from the adapical side it shows a large central cavity, with calcified walls, filled with darkly stained tissue, unlike that of the surrounding zooids. It is surrounded by one pair of very small zooids on one side, and a pair of slightly larger zooids on the other side. It is possible that the central cavity represents a primary rootlet element arising from a kenozooid.

The presence of rootlet pores in the early astogenetic stages of *Trochosodon* suggests that the analogous series of apical structures and the primary kenozooid in species without rootlet pores fulfil a similar function, especially as the colonies inhabit similar environments (see also p. 346).

The ancestrular area of conescharelliniform colonies is considered apical in the geometric sense. In the bilaminar orbituliporiform colonies the theoretical colony cone may be regarded as bilaterally compressed, with a consequent distortion of the apical region to one side of the colony. Development of kenozooidal and/or extra-zooidal tissue complicates the structure of the apical region in both groups.

The exact nature of the ancestrula is not known, and as the calcified parts of the colony are not attached to, nor incorporate a recognizable substratum (as, for example, in the Cupuladriidae, which incorporate a small sand grain or foraminiferan), the earliest astogenetic changes may only be inferred. It is probable that a single
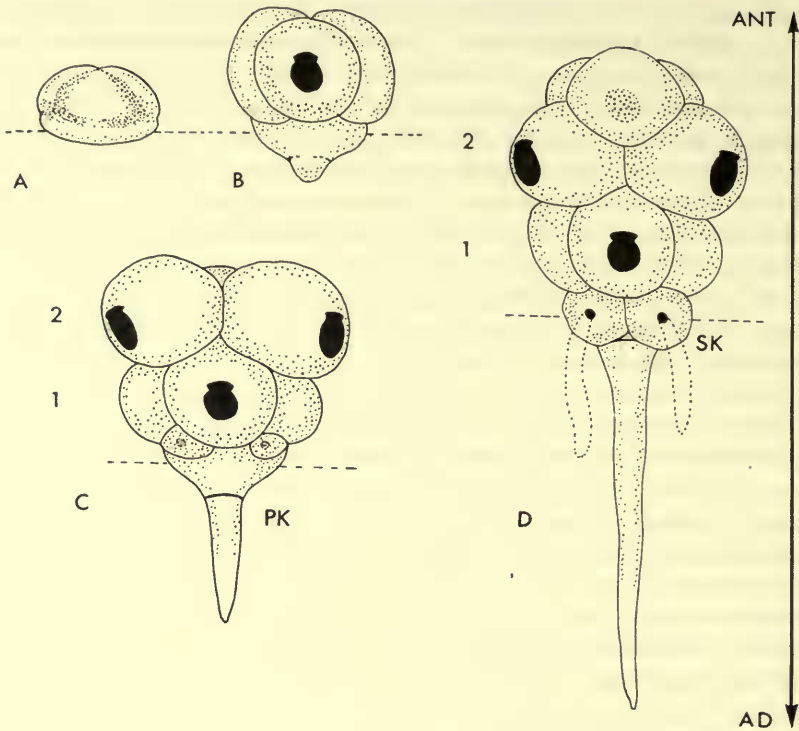
Fɪɢ. 4.   Hypothetical early astogeny of a conescharelliniform colony, assuming that the
    apical tube produces rootlets anchored in a soft substratum.   The orientation in life is
    unknown, but this form of astogeny would be applicable if the colonies were suspended by
    rootlets.   AD, adapical direction ; ANT, antapical direction ; PK, primary kenozooidal
    rootlet ; SK, secondary kenozooidal rootlet ; 1, first zooid whorl ; 2, second zooid whorl.
        A. Metamorphosed larva producing an ancestrular complex comprising one kenozooid
    and three zooid elements.   B. First whorl of zooids complete, kenozooidal tube developing
    and forming primary rootlet.   C. Second whorl of zooids complete, apical kenozooids
    forming round apical kenozooidal tube.   D. Third whorl of zooids developing, apical tube
    now comprising several secondary kenozooids with secondary rootlets.

ancestrula with calcified walls is not developed at metamorphosis.   Instead the
primary whorl of zooids or kenozooids may be simultaneously differentiated within
an uncalcified ancestrular complex which also includes a rootlet element.   Develop-
ment of such a kenozooidal rootlet or rootlets would rapidly separate the budding
locus from the substratum, into which the rootlet system would become attached or
anchored.   Later development of apical kenozooids could also provide further
rootlets, while the primary zooid whorl budded successive generations of zooids
frontally in the opposite direction (see Fig. 4).   This would account theoretically
both for the inferred method of life, and for the absence of a substratum attached to
a single, calcified ancestrula.   Ancestrular complexes of 2–4 zooids are known (see
Eitan, 1972, and Cook, 1973).   Rootlet development may be very rapid.   For

example, living colonies of *Hippopetraliella africana* from Ghana have been seen to develop basal rootlets 5 mm long in 48 hours. Opposing directions of growth from an ancestrular focus were described by Harmer (1957 : 794–795) for colonies of *Adeona* with complex systems of kenozooidal rootlets. Bryozoan colonies may also be established by kenozooids, feeding zooids not appearing until later astogenetic stages, as in *Scruparia*. Thus the necessary elements for the hypothetical astogeny given in Fig. 4 do occur in Bryozoa, although they have not all been directly observed in such a combination.

A demonstration by Dr G. Eitan, exhibited in September 1974 at the 3rd International Conference of the International Bryozoology Association (Department of Geology, Université Claude-Bernard, Lyon), showed that the early astogeny of *Margaretta*, an erect jointed form, was very similar to that postulated for conescharelliniform colonies. The ancestrular complex included kenozooidal rootlets, and was adhesive, but not adherent to the substratum.

Lagaaij (1963b : 203–207), discussing the possible mode of life of *Fedora*, postulated anchoring rootlets arising from 'special chambers' associated with the zooids. One such chamber was observed with a fine, cuticular rootlet intact. He also described colonies which had incorporated fine grains of substratum material. One colony of *Batopora clithridiata* (see p. 351) from the Eocene (Hampstead, London Clay, BM 69554 pt.) shows a similar growth form. At some point in its astogeny the colony has incorporated a small sand grain, 0·60 mm in diameter. The apical zooids surround part of the sand grain, but are very irregular in shape and may belong to a secondary zone of change. The remaining zooids are budded frontally in regular alternating series.

COMPARISON OF ASTOGENETIC SERIES

Astogenetic series within a single population are rare, but it has been possible to trace the astogeny almost completely in *Lacrimula asymmetrica* (see p. 361) and partially in *L. grunaui*. Comparison of the number of zooids per whorl with the number of whorls and the total number of zooids in a colony has shown that there are some fundamental differences among species which are related to their astogeny.

For example, if there is little increase in the number of zooids per whorl throughout astogeny in the primary zones of change, the number of zooids in a colony should increase arithmetically. Differences between estimated and actual totals should be attributable to other observable astogenetic changes. This hypothesis was tested in samples which contained several colonies at different astogenetic stages (see Table 1).

In *Batopora murrayi* the number of zooids falls below that estimated because avicularia and kenozooids actually take the place of entire zooids in series. In *B. stoliczkai* the primary triad comprises one kenozooid and two zooids, and in both *B. stoliczkai* and *B. clithridiata* the actual number increases rapidly above the estimated figure as scattered, secondary frontally budded zooids occur with greater frequency. The same reason for increase occurs in one *B. rosula* colony from Crete. The larger colonies from Baden appear to have only four zooids per whorl in the

TABLE I

Comparison of astogenetic series

	No. of zooids per whorl	No. of whorls	Estimated no. of zooids	Total observed no. of zooids
Batopora murrayi	5	3	15	15
	5	4	20	18
	5	5	25	20
B. stoliczkai	3	3	8	8
(first whorl has	3	4	11	15
two zooids only)	3	5	14	18
	3	6	17	22
	3	7	20	30
B. clithridiata	4	3	12	13
	4	4	16	18
	4	5	20	28
	4	6	24	33
B. rosula (Crete)	5	4	20	21
	5	8	40	38
B. rosula (Baden)	4	4	16	17
	5	4	20	21
	7	4	28	30
	7	7	49	48
B. multiradiata	7	6	42	43
	7	7	49	49
	7	9	63	66
	7	12	84	80
	4	6	24	56
	4	8	32	60
	4	11	44	66
Lacrimula asymmetrica	5	1	5	5
	4	2	9	9
	5	3	14	14
	4	4	18	18
	5	5	23	23
	4	6	27	27
L. grunaui	4	5	20	20
	4	6	24	24
	4	9	36	36
L. perfecta	5	6	30	30
	6	6	36	36
	6	8 (estimated)	48	46
	9	11 　 ,,	99	86
	9	20 　 ,,	180	160

first whorl, but there does seem to be a production of intercalary series of zooids in the primary zone of change, which accounts for the larger totals at the same astogenetic stage as the remaining colonies from Crete. The actual numbers may fall below the estimated numbers because the production of intercalary series is not absolutely regular. Young stages of *B. multiradiata* resemble some of the larger colonies of *B. rosula* from Baden in number of zooids, which is very close to the estimated figure. They may be distinguished from nearly all other specimens of *Batopora* by the number of zooids per whorl. The colony and zooid size is, however, small. Young colonies with six to seven zooid whorls comprise 43–49 zooids ; a colony of *B. scrobiculata* of comparable size (about 1 mm high and 2 mm wide) has only 24 zooids, and one of *B. murrayi* only 15. The colonies of *B. grandis* differ completely in their very large number of zooids yet apparently low number of zooids per whorl.

In *L. burrowsi* and *L. perfecta*, the proliferal region, comprising relatively few zooids of the primary zone of change, merges with a secondary zone of change, including intercalary rows, and contains a larger number of zooids.

In *L. perfecta* the apical region is rapidly covered by a proliferation of kenozooids, and the number of whorls in this region has been estimated by comparison with younger colonies. The actual number of zooids is less than that estimated, as the number of zooids in the primary whorl is unknown in large colonies, but due to the introduction of intercalary rows, is less than that in the proliferal region, on which the estimate for the whole colony is based.

In *L. asymmetrica* the number of zooids per whorl regularly alternates between four and five, because one zooid is always developed slightly earlier than the others in alternate whorls. The number does not increase arithmetically, but the agreement between the estimated and actual numbers in these colonies and those of *L. grunaui* is a measure of the regularity of growth and the absence of any secondary zooids at these astogenetic stages.

CODING OF CHARACTERS AND RESULTS OF POLYTHETIC CLUSTERING

The advantages of studying morphological relationships of bryozoan populations by polythetic clustering have recently been discussed by Cheetham (1968) and by Boardman *et al.* (1969). Apart from supplying a visual display of degrees of morphological similarity it may reveal new aspects of problems which have been hidden by previously accepted taxonomic concepts. In addition, the discipline of producing a coding for comparison of characters means that the basic nature of the 'characters' themselves is re-examined and that the specimens are subjected to a consistent series of observations and analysis (see Boardman *et al.*, 1959, fig. 1).

After analysis and clustering, under ideal conditions, the morphological relationships displayed can be tested for systematic relevance by plotting the clusters in a time-space context (see Boardman *et al.*, 1969, figs 11 and 12).

During work on the conescharelliniform species described here, we became aware of a number of exceptions to the generally accepted character-correlations within the populations studied. This was particularly noticeable when specimens were being

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assigned to nominal genera using the classical concepts of such groups. Great variation within samples of what appeared to be 'species' was also found, although to some extent this could be attributed to astogenetic and ontogenetic differences.

Some characters are listed in Table 2, and their occurrence compared among species assigned to the genera illustrates how arbitrary some of our decisions have been.

TABLE 2

Occurrence of characters among species.

	Conescharellina	Batopora	Lacrimula	Atactoporidra
1. External apical tube	1 species	B. rosula B. multiradiata B. grandis	all species	A. bredaniana
2. Colony-wide secondary zones of zooids	absent	B. multiradiata	L. asymmetrica L. similis	all species
3. Rootlet pores (lunoecia)	nearly all species	absent	absent	absent
4. Axial kenozooids	nearly all species	B. rosula B. scrobiculata B. asterizans	L. perfecta L. visakhensis L. similis	absent
5. Avicularia	all species	B. murrayi B. clithridiata	nearly all species	A. bredaniana
6. Condyles	all species	absent	nearly all species	?
7. Sinus	all species	B. grandis	L. asymmetrica L. grunaui L. similis	absent
8. Ovicells laterally displaced	C. catella	B. grandis	not displaced	not displaced
9. Ovicells apical	C. africana	not apical	L. visakhensis	not apical

In order to test concepts of both 'species' and 'genera', characters were chosen, analysed and used to assess similarity among the specimens examined. One of the most useful results of this analysis has been the demonstration of factors which must be considered both when deciding character states and when interpreting the clusters.

The biology of living specimens of conescharelliniform species is virtually unknown, and the characters used here, both quantitative and qualitative, represent only a small part of those potentially available in Bryozoa. Much finer examination of plentiful colonies may reveal, for example, characters associated with calcification of walls, intercommunication of zooids, and detailed structure of orifices, avicularia and ovicells. Further information may come from investigation of the astogenetic and ontogenetic changes occurring in the apical region.

We are here dealing with Bryozoa in which both the sample and colony size are often very small. The interaction of genetic relationships and environmental influences has apparently evolved great similarity in colony structure and zooid form among samples. Conversely, astogenetic and ontogenetic changes produce large morphological differences within samples. For example, one possibility arising from comparison of colonies at different astogenetic stages, or where relative astogenetic ages cannot be inferred, is that clusters may reflect age similarities more than 'taxonomic' similarities.

Comparison of characters of similar astogenetic age is difficult, as a zone of repetition is not usually present. Although both absolute and relative rates of astogenetic and ontogenetic change are unknown, one approximate guideline available is the comparison of colonies with the same, or nearly the same, number of zooid whorls. Because colonies rarely bud in regularly alternating or direct patterns (see p. 324), it is not always easy to decide how many zooid generations are present, and because the numbers of whorls is often low, errors are correspondingly significant. Much of the material examined is fossil, and differences among and within samples may therefore be partly the result of differential conservation. Characters and character states used are given in Table 3, and a list of the specimens in Table 4 (see also Appendices 1–3). The following notes explain some of the concepts used in defining the characters, and why difficulties were sometimes encountered in deciding which of the character states was present.

Characters 1 *and* 2. The axial length and proliferal region width of a colony not only give a measure of absolute size, but describe its shape. In conjunction with the number of zooid whorls it also gives a secondary measure of zooid size range and arrangement.

Characters 3, 4, 14, 27 *and* 28. The type, number, position and nature of astogenetic zones. All colonies comprise at least one zone of change. Coding the presence of secondary zones was confined for these characters to those consisting of zooids only. The kenozooids, interzooidal avicularia and apical structure are considered separately, as it is not known exactly when and in what sequence these may be secondary in occurrence. The numbers of whorls of zooids is counted as the number of series which it is inferred were budded simultaneously, whether alternately or directly. The number of zooids in each whorl can be inferred from the proliferal region, and in many colonies is the same or very few more than the number in the primary whorl.

Character 5. Number of zooids at the surface. Here only forms with one zone of change are strictly comparable, but the presence of very large numbers of zooids is often directly correlated with the presence of a secondary zone of change or zone of repetition.

Characters 6, 7, 10 *and* 11. The maximum length and width of exposed frontal wall. This is the equivalent of the 'classical' zooid length and width usually measured for cheilostomes. Where possible, the measurement of the third whorl zooids was taken as this gives one of the few estimates of size among colonies at a comparable astogenetic stage. The size of the subproliferal zooids is correlated with the number of whorls and the size and astogenetic age of the colony, and gives an estimate of the

TABLE 3

Characters and character states

Character	As measured or counted	State 0	State 1	State 2	State 3
1. Axial length of colony (AxL)	,,				
2. Width of proliferal region (Prl)	,,				
3. Number of whorls of zooids	,,				
4. Number of zooids/whorl	,,				
5. Number of zooids at colony surface	,,				
6. Length of exposed frontal wall of zooid of third whorl	,,				
7. Width of same	,,				
8. Length of orifice of same	,,				
9. Width of orifice of same	,,				
10. Length of exposed frontal wall of zooid of subproliferal whorl	,,				
11. Width of same	,,				
12. Length of orifice of same	,,				
13. Width of orifice of same	,,				
14. Number of zones of astogenetic change (excluding kenozooids)		'pit' obscured by kenozooids	one zone of change	more than one zone of change	plus zone of repetition
15. Nature of apical region			'pit'	external tube	secondarily budded kenozooid

No.	Character						
16.	Length of apical tube or kenozooid	"	"				
17.	Width of apical aperture	"	"				
18.	Inflation of exposed wall of subproliferal zooid				flat	slightly inflated	distinctly inflated and prominent
19.	Calcification of same				smooth, tubercles <5 μ	finely granular, 5–20 μ	coarsely granular, >20 μ
20.	Condyles in orifice			absent or not seen	present		
21.	Sinus in orifice			absent or not seen	wider than half width of orifice	narrower than half width of orifice	
22.	Position of kenozooids or closed zooids			absent	apical only	apical and/or scattered adventitious	as 2 + axial
23.	Avicularia			absent	interzooidal	adventitious	
24.	Ovicells			absent	present		
25.	Length of subproliferal ovicell	"	"				
26.	Width of subproliferal ovicell	"	"				
27.	Position of origin of secondary zone zooids			absent	adapical	scattered	antapical
28.	Nature of secondary zone zooids			absent	frontally budded	overgrowth	

TABLE 4

List of specimens analysed
(see also Fig. 5)

Number	Asto-genetic group	Name	Reference	Locality	Age
1	A	*Batopora multiradiata*	K 48–50	Spain	Oligocene
2	B	,, ,,	USNM 71205	Italy	Eocene
3	B	,, ,,	USNM 88881	,,	,,
4	A	,, ,,	USNM 71205	,,	,,
5–6	B	,, ,,	USNM 88881	,,	,,
7	D	*Batopora scrobiculata*	USNM 88882	Bavaria	,,
8	B	*Batopora grandis*	,, ,,	,,	,,
9–10	C	,, ,,	,, ,,	,,	,,
11	B	,, ,,	,, ,,	,,	,,
12	B	,, ,,	BM D31117	,,	,,
13	A	*Batopora multiradiata*	USNM 71205	Italy	,,
14 & 16	A	*Atactoporidra bredaniana*	BM D7864	Belgium	,,
15	B	,, ,,	,, ,,	,,	,,
17–18	A	*Lacrimula burrowsi*	BM 1965.8.24.11	Zanzibar	Recent
19	B	,, ,,	BM Stn 103	,,	,,
20–21	A	,, ,,	,, ,,	,,	,,
22	C	*Lacrimula pyriformis*	BM 1965.8.24.13	,,	,,
23	B	,, ,,	,,	,,	,,
24	D	*Lacrimula* sp.	BM Stn 98	,,	,,
25–26	C	,, ,,	,,	,,	,,
27	B	,, ,,	BM Stn 126	,,	,,
28–30	C	*Lacrimula visakhensis*	BM 1970.8.8.1	E. India	Holocene
31 & 33	C	*Lacrimula similis*	BG 312	Indonesia	Miocene
32	B	,, ,,	,,	,,	,,
34–35	D	*Lacrimula asymmetrica*	,,	,,	,,
36–37	C	,, ,,	,,	,,	,,
38	D	*Lacrimula grunaui*	G 5671	,,	,,
39	C	,, ,,	,,	,,	,,
40	B	,, ,,	,,	,,	,,
41	D	*Lacrimula borealis*	43/3–1	North Sea	Oligocene
42	D	*Batopora* sp.	SM 55	Italy	Miocene
43	C	*Batopora rosula*	6–27	Crete	,,
44	D	,, ,,	,,	,,	,,
45	D	,, ,,	Huelva	Spain	Pliocene
46	D	,, ,,	PLR 4607	Malta	Miocene
47	C	,, ,,	R1103	Spain	,,
48–49	D	*Batopora murrayi*	BM1965.8.24.6	Zanzibar	Recent
50–52	D	,, ,,	BM Chall. 174D	Fiji	,,
53	D	*Batopora rosula*	NMV fig. 7	Austria	Miocene
54	C	,, ,,	NMV fig. 1	,,	,,
55–56	D	,, ,,	NMV	,,	,,
57	A	*Batopora multiradiata*	BM	Italy	Eocene
58	C	*Trochosodon* sp.	BM Stn 126	Zanzibar	Recent
59	D	*Batopora clithridiata*	BM B1357C	England	Eocene
60	D	,, ,,	BM D40339	,,	,,
61	C	,, ,,	BM B1357	,,	,,

TABLE 4 (cont.)

Number	Asto-genetic group	Name	Reference	Locality	Age
62	C	*Batopora asterizans*	K 52	Netherlands	Oligocene
63	D	,, ,,	,,	,,	,,
64	D	,, ,,	43/3−1	North Sea	,,
65	D	*Lacrimula perfecta*	BM	Italy	Eocene
66−67	C	,, ,,	,,	,,	,,
68	C	*Conescharellina africana*	BM 1949.11.10.639	Durban	Recent
69	B	,, ,,	,,	,,	,,
70−72	C	*Batopora stoliczkai*	NMV	Bünde, Germany	Oligocene
73−74	C	,, ,,	USNM	Calbe, Germany	,,
75 & 77	C	,, ,,	NMV	Bünde, Germany	,,
76	D	,, ,,	,,	,,	,,
78	C	*Batopora* sp.	,,	,,	,,
79	D	,, ,,	,,	,,	,,
80	A	*Atactoporidra glandiformis*	BM D30077	England	Eocene

rate of astogenetic change when compared with the third whorl measurements. In a few cases, both sets of measurements are identical, as only four whorls were present.

Characters 8, 9, 12 *and* 13.   The size of the orifice generally increases with each whorl ; the characteristics of these measurements are similar to those of the exposed frontal wall.

Characters 15, 16, 17 *and* 22.   The astogeny of the apical region.   This is not easily inferred and the choice of states is somewhat arbitrary.   In some forms of *Batopora*, *Lacrimula* and *Atactoporidra*, distinct units of calcification, presumably kenozooids, each with a small central pore, form the apical region as an external tube.   In other forms such kenozooids are absent and the tube appears to be extrazooidal in structure, or an internal tube is present, which may also be composed of either kenozooidal or extrazooidal tissue.   The correlation of types of structure with astogenetic age or sample is not clear.   In *Batopora*, the internal tube may be obscured by kenozooids, or replaced by a secondarily budded kenozooid which may or may not be surrounded by other small kenozooids.   In some samples an astogenetic series is present which enables the sequence of appearance of the structures to be inferred, but generally there is a great deal of variation.   Kenozooids and extra-zooidal tissue tend to merge with closed zooids in the apical region.   In *Lacrimula*, closure consists of a calcified lamina filling the zooidal orifice, often leaving a small pore or slit centrally.   Small kenozooids are often found among the zooids in *Batopora*, presumably budded frontally, but whether secondary to the primary zone of zooids is not known.   They may occur adapically to antapically, and in some forms appear antapically in the axial region of the proliferal zooids.

Character 18.   Inflation of the frontal walls.   Inflated walls are positively correlated with long, tubular peristomes in Recent forms.   Fossil specimens are usually worn but the subproliferal zooids may show distinct states of inflation and sometimes elongated peristomes.

Character 19.   The degree of tuberculation of the exposed frontal wall may be affected by preservation.   The majority of colonies thus appear to be 'finely granular,' but some are consistently smooth and others coarsely granular.

Character 23.   Avicularia are not generally common and are usually interzooidal, budded frontally among zooids in a similar manner to the kenozooids.   Structures inferred to be adventitious avicularia are very rare and occur in one species only ; they are associated with the edge of the peristome.

Characters 24, 25 *and* 26.   All ovicells seen are hyperstomial and usually appear to have been closed by the operculum.   Some are large and prominent, others small and immersed, a few are laterally displaced.   The presence of ovicells may indicate astogenetic maturity, and they are often present only in the proliferal region.

   Ideally, comparison should be made only among colonies from each sample which are at exactly the same astogenetic stage, but this was not possible with the material available.   Eighty colonies were therefore divided into four groups of roughly comparable astogenetic age.   The division was not completely arbitrary, but endeavoured to include colonies from as many samples as possible in each group (see also Table 4).

Group A comprised 11 colonies with 15–22 astogenetic generations from 7 samples. 3 of which were also represented in Group B.
   (Nos 1, 4, 13, 14, 16, 17, 18, 20, 21, 57, 80.)

Group B comprised 14 colonies with 9–13 astogenetic generations from 11 samples, 3 of which were also represented in Group A, 6 in Group C and 1 in Group D.
   (Nos 2, 3, 5, 6, 8, 11, 12, 15, 19, 23, 27, 32, 40, 69.)

Group C comprised 31 colonies with 6–8 astogenetic generations from 18 samples, 5 of which were also represented in Group B, and 10 in Group D.
   (Nos 9, 10, 22, 25, 26, 28–31, 33, 36, 37, 39, 43, 47, 54, 58, 60–62, 66, 67, 68, 70–75, 77, 78.)

Group D comprised 24 colonies with 3–5 astogenetic generations from 18 samples, 10 of which were also represented in Group C, and 1 in Group B.
   (Nos 7, 24, 34, 35, 38, 41, 42, 44–46, 48–53, 55, 56, 59, 63–65, 67, 79.)

FIG. 5.   Ordination diagrams, prepared by the principal co-ordinates algorithm (Gower, 1966).   Squared distance in proportion to (100-similarity).   See Table 4 for key to numbering ; data and co-ordinates stored at BMNH.
   A. Group A colonies with 15–22 zooid whorls.   Co-ordinates 1 & 2, 1 & 3 and 3 & 2. Note complete separation of clusters of *B. multiradiata* (1,4,13,57), *Atactoporidra* (14,16,80) and *Lacrimula* (17,18,20,21) in three dimensions.
   B. Group B colonies with 9–13 zooid whorls.   Co-ordinates as above.   Note degree of separation similar to that in Group A of clusters of *B. multiradiata* (2,3,5,6) *Lacrimula* (19,23,27) and *Atactoporidra* (15).   *B. grandis* (8,11,12), *L. grunaui* (32,40) and *Conescharellina africana* (69) are also completely separated in three dimensions.
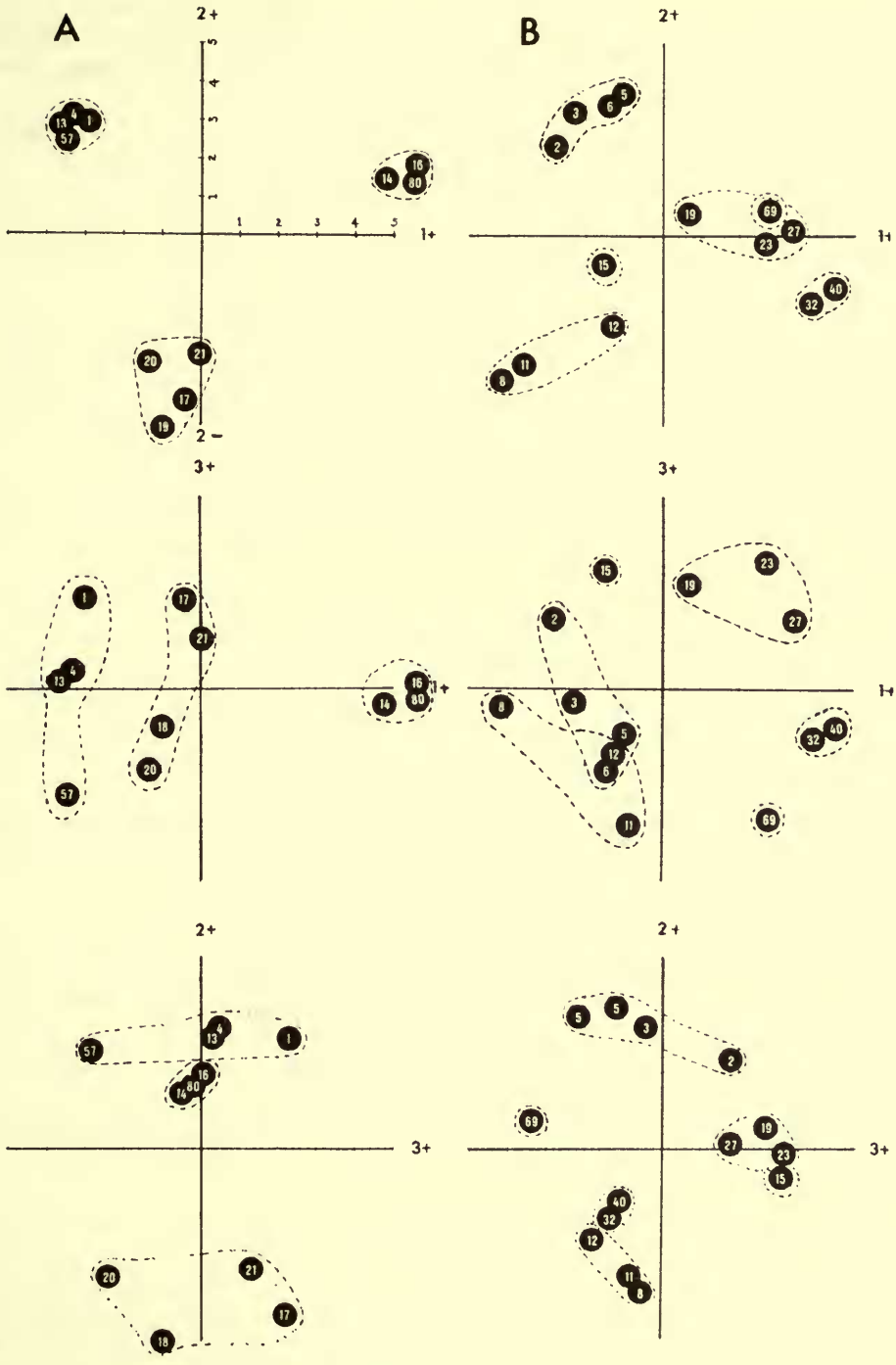
Results

In Group A, separation of three-dimensional clusters of the large colonies in samples of *B. multiradiata*, *L. burrowsi* and *Atactoporidra* was distinct. Within *Atactoporidra*, both species clustered together (see Fig. 5A).

In Group B, smaller colonies of *B. multiradiata*, *A. bredaniana* and *Lacrimula* maintained a similar degree of separation to that of Group A, except that within *Lacrimula*, two clusters, one of *L. burrowsi* and *L. pyriformis*, the other of *L. similis* were formed. Colonies of *B. grandis* also formed a distinct cluster (see Fig. 5B).

In Group C, a much larger number of still smaller colonies were compared, and the resulting clusters were far less distinct. *B. grandis*, *B. clithridiata* and *B. rosula* formed consistently separated clusters, but the variation within several of the other samples was apparently greater than the difference among samples of different nominal species. For example, three widely separated and variably constituted clusters of several species of *Lacrimula* were formed, and two distinct clusters of *B. stoliczkai*, one of which included *B. asterizans*.

In Group D, this within-sample diversity was maintained in *Lacrimula*. *B. rosula*, however, formed a distinct cluster, but included *L. borealis*, just as the very loose cluster of *B. murrayi* included *B. clithridiata*. *B. asterizans* again clustered with *B. stoliczkai*.

Some of this apparent confusion can be attributed to the general similarity of these very small colonies, the differences in total numbers and overall dimensions of zooids etc. being much less in groups C and D than in A and B. Ontogenetic differences such as presence or absence of ovicells also produced relatively large differences within samples which outweighed similarities in other characters. It is probable that if additional characters, and a larger number of colonies from each sample were available, the resulting clusters might be less diffuse.

Generally, the interpretation of these three-dimensional clusters has confirmed the degrees of difference among the samples reached by inspection. Until further work can be done, using a more thorough analysis of larger samples, few systematic relationships in time can be demonstrated here.

The Eocene to Oligocene samples of *B. multiradiata* may be confidently inferred to be genetically continuous, as may the Miocene to Pliocene samples of *B. rosula*. There is a very close relationship between the Oligocene *B. stoliczkai* and *B. asterizans*, and a more tenuous link may perhaps be indicated between these populations and the Eocene *B. clithridiata*. Relationships within *Lacrimula* are obviously very complex, and intermediate forms in time and space are required to establish any pattern of relationship both among the Eocene to Recent forms, and between *Lacrimula* and *Conescharellina*.

EVOLUTIONARY TRENDS IN MORPHOLOGY

Batopora, appropriately named after the blackberry, shows little evolutionary change with time. At most there is a tendency towards increasing regularity in the arrangement of the radial rows of zooids around the colony axis, but on the other hand good regularity is already present in an early, Middle Eocene (Lutetian), form

like *B. scrobiculata* Koschinsky. *B. multiradiata* would seem to be an exception, with its very irregular, double-layered arrangement, and large number (120 or more) of zooids per adult colony. This irregularity is however more apparent than real (see p. 350). In most other species of *Batopora* the number of zooids fluctuates from 13 to 48 (see Table 1). There is not much of an evolutionary trend to be found in the development of either kenozooids or heterozooids. Kenozooids on the antapical surface are already mentioned in the original descriptions of the Late Eocene *B. multiradiata* and of the Oligocene *B. stoliczkai*. In the latter species other kenozooids occur among the zooids on the opposite, conical surface, just as they do in the Recent *B. murrayi*. Avicularia with a cross-bar, which occasionally occur among the zooids in the last species, are rare in the genus but also occur in one of the earliest forms, the Eocene *B. clithridiata*.

In *Lacrimula*, the principal change with time appears to be the loss of axial kenozooids, which are present in the Upper Eocene *L. perfecta* but absent in some Miocene and all Recent forms. This trend is not a simple one, however, as axial kenozooids are present in the Holocene *L. visakhensis* and the Miocene *L. similis*, but absent in the Oligocene *L. borealis*. Although one sample of *L. perfecta* contains fairly large colonies, there does also seem to have been a general increase in maximum colony size with time.

ECOLOGY AND PALAEOECOLOGY

Conescharelliniform, orbituliporiform and generally lunulitiform colonies are classically associated with calm, often deeper water, and sands, i.e. coarser-grained sediments. The evidence given below includes lithology, known and inferred depth and assemblages of Recent and fossil forms.

Nearly all Recent records of species with these three colony forms are associated with sea-bottoms of sand or mud. Lagaaij (1963a) gave details of the limits of tolerance in *Cupuladria*, and Cook (1963, 1966) has noted similar associations. The distribution of Recent *Conescharellina* is almost confined to sandy and muddy sea-bottoms (see Station data given by Canu & Bassler, 1929 ; Silén, 1947 ; Harmer, 1957). The lithology of fossil colonies shows a similar range of grain size, from calcarenite to clay (see Table 5).

Recent *Conescharellina* occurs in depths which vary from 12 m to more than 2000 m. Most records are from the range 140–450 m. Recent *Lacrimula* occurs from approximately 100 to 200 m, and *Batopora* from 285 to 805 m. Other conescharelliniform genera such as *Fedora* have been found at 2018 m (see Jullien, 1883), and *Trochosodon* occurs from 88 to 2081 m, the majority of records being from the deeper end of this range (see Harmer, 1957 : 744 for details).

Fossil records of *Batopora* carry with them the connotation of occurrence at relatively great depths. Namias (1891 : 506), for example, reported *B. rosula* from 'stradi di mare profondo' and Seguenza (1880 : 130) reported *B. rosula* as one of the commonest, and always perfectly preserved species of Bryozoa in the Tortonian clays at Benestare, Calabria, which he considered (p. 90) 'un deposito di mare considerevolmente profondo'. Le Saint (1961 : 96) referred to 'la préférence de ses

formes [Batopora] pour les eaux relativement profondes'. Some occurrences of *Batopora*, however, may be inferred to be relatively shallow and neritic, two of the shallowest being (1) that of *B. rosula* with numerous *Cupuladria haidingeri*, some *C. canariensis* and some *Biflustra texturata* in the upper part of the Middle Tortonian Tefeli Formation, Almiri Section, Iraklion Province, Crete; Sissingh (1972 : 33) referred to these beds as 'deposited in a marine environment of shallow to moderately deep water'; (2) that of *B. multiradiata* in the Lower Oligocene calcarenites of Moli de Llinares, north of Villajoyosa, Alicante Province, Spain. The associated rich and diversified larger Foraminifera assemblage was listed by Cosijn (1938 : 13) and guarantees non-bathyal depth, although MacGillivray (1971 : 236) remarked, 'the formations have characteristics of gravitational deposits', i.e. may have been secondarily displaced into deeper waters. The deepest bathyal occurrences which may be inferred, on the other hand, are found in (1) the Torre Veglio Section, northern Italy, in a wash residue consisting almost entirely of planktonic Foraminifera (Schüttenhelm, pers. comm.); (2) the INI–Coparex Huelva–1 well, at 648 m below surface, in the Cadiz Basin, Spain, associated with a flood of planktonic Foraminifera and with common *Liebusella soldanii*.

TABLE 5

Correlation of sediment type, depth and assemblage of
conescharelliniform colonies

Name	Reference	Age	Type of sediment	Type of assemblage	Depth (known or inferred)
Batopora clithridiata	Gregory, 1893	Early Eocene	C	O : S	
B. stoliczkai	Labracherie, 1961	Early to Middle Eocene	? AS	(M) : S	
Atactoporidra globosa	Labracherie, 1961	Early to Middle Eocene	? AS	O : S	
B. scrobiculata	Koschinsky, 1885	Middle Eocene		O : S	
A. glandiformis	Cheetham, 1966	Middle Eocene	C	O : S	55–90 m
B. multiradiata	Reuss, 1867	Late Eocene	M	O : S	
B. rosula	Malecki, 1963	Late Eocene	CS	O : S	
B. stoliczkai	Malecki, 1963	Late Eocene	CS	O : S	
Lacrimula perfecta	Accordi, 1947	Late Eocene		O : S	
A. bredaniana	Dartevelle, 1933	Late Eocene to Early Oligocene	? AS	O : S	
B. multiradiata	K 48–51, Spain	Early Oligocene	CR	O	Shallow to moderately deep
L. borealis	43/3–1, North Sea	Middle Oligocene	C	(M) : S	
B. asterizans	Boom Clay	Middle Oligocene	C	M	150–250 m (Boekschoten, 1967)
B. stoliczkai	Reuss, 1867	Late Oligocene		S	
Batopora sp.	Cheetham & Håkansson, 1972	Late Oligocene	C	O	150–200 m

TABLE 5 (*cont.*)

Name	Reference	Age	Type of sediment	Type of assemblage	Depth (known or inferred)
B. rosula	R 1103, Spain	Early Miocene	C	(M)	
B. rosula	SM 55, Italy	Early Miocene	M	M	Bathyal
B. multiradiata	Ceretti & Poluzzi, 1970	Early Miocene	CR	O	
B. rosula	MU 214, Sardinia	Early Miocene	M	M	
L. asymmetrica	BG 312	Early Miocene		S	
L. similis	BG 312	Early Miocene		S	
B. rosula	PLR 4067, Malta	Middle Miocene	C	M	
B. rosula	Reuss, 1848	Middle to Late Miocene	C	(M) : S	Bathyal (Haug, 1920 : 1637)
B. rosula	Seguenza, 1880	Middle to Late Miocene	C		
B. rosula	6–27, Crete	Late Miocene	M	M	shallow to moderately deep
B. rosula	Huelva, Spain	Pliocene	FS	M	Bathyal
L. visakhensis	Rao & Rao, 1973	Holocene	CS	O : S	89 m
B. murrayi	Cook, 1966	Recent	C	M	805 m
L. burrowsi	Cook, 1966	Recent	CS	O : S	101–207 m
L. pyriformis	Cook, 1966	Recent	CS	O : S	310 m
Conescharellina africana	Cook, 1966	Recent	Md	O : S	102 m
C. angustata	Harmer, 1957	Recent	Md	O : S	88 m
Trochosodon radiatus	Harmer, 1957	Recent	Md	M	1944 m

Sediment :
CR = Calcarenite ; C = Clay ; Md = Mud ; M = Marl ; FS = Fine-grained sand ; AS = Argillaceous sand ; CS = Coarse-grained sand.
Assemblage:
M = Monospecific ; (M) = Almost monospecific ; O = Multispecific assemblage ; S = Other specialized colony forms present in assemblage, i.e. orbituliporiform or lunulitiform colonies.

Generally, both fossil and Recent bryozoan assemblages associated with soft and unstable sea-bottoms show first an increasing number of specially adapted forms with increase in depth. This is followed by a decrease in all forms ending in mono-specific occurrences at very great depths.

Harmer (1957 : 649–650) analysed the species obtained by the 'Siboga' from a few stations in the Java Sea where the sea-bottom was mud at 82–88 m ; he remarked : 'There is no group of Stations . . . in which the correlation between mode of growth and nature of the bottom is more clearly established.' Of the 39 species found, many were new, and at least 15 showed some recognizable adaptation to the specialized conditions. Eight had some form of rootlet system and six were

lunulitiform species.   As *Conescharellina* and *Flabellopora* are known to have rooting systems which can be associated with foraminiferal ooze, it is interesting to note the close correlation of their distributions.   These two genera, often represented by several species, occur together at 20 of 36 stations listed by Canu & Bassler (1929), Silén (1947) and Harmer (1957).   In addition, *Lanceopora* occurred with the above genera at eight of these stations.

Recent and Holocene records of *Lacrimula* are correlated with *Cupuladria* and *Conescharellina*.   *Conescharellina* and *Trochosodon* have been found in association with as many as seven other similarly adapted species at the shallower end of their range.   At great depths, both these genera tend to have monospecific occurrences, and, as noted above, one record of Recent *Batopora* is from very deep water.

Evidence from fossil assemblages gives a similar picture.   Maplestone (1904 : 207, 209) gave tabulations which noted the correlation of fossil *Conescharellina* and *Lanceopora* (as *Schizoporella flabellata*, see also Maplestone, 1910).   Among the specially adapted forms such as *Kionidella*, *Stichoporina* and *Lunulites*, *Orbitulipora* is one of the commonest genera found in association with specimens of *Atactoporidra* and *Batopora* (see, for example, Ossat & Neviani, 1897 ; Gregory, 1893 ; Malecki, 1963 ; Labracherie, 1961).

Batopora multiradiata is generally associated with diversified bryozoan faunas, but the three very deep records of *Batopora* mentioned above, two fossil and one Recent, are conspicuously monospecific, and it is only one step further to suggest that *all* monospecific occurrences come from the deep end of its bathymetric range. There is nothing in the data at hand (Table 5) to contradict this suggestion.   The Lower and lower Middle Miocene of the Mediterranean area seem to be particularly marked by such monospecific deep-water occurrences, and in keeping with the inferred depth, the associated lithologies tend towards the finer grain-sizes ; either marl or calcareous clay (Table 5).

DISTRIBUTION IN TIME AND SPACE

Historically, the oldest published record of a conescharelliniform colony is that of *Batopora*, in Soldani's figure of '*Historices marinas minimas*' (Soldani, 1780, pl. 16, figs 83Q, R ; figures copied by Annoscia, 1968, pl. 1, figs 8a, b).   According to the original plate explanation (p. 130) these fossils originate from 'the valley East of San Quirici'.   Dr Annoscia kindly informs us that 'The location of the samples containing *Batopora*, according to Soldani's words, is "not far from Caitro [nowadays unknown] S. Quirico, in a place above the Fosso di Rifigliuoli [now 'Fosso Refiglioli' see map] named Poggi di Rifigliuoli (Soldani, 1780, pp. 130 e 35, art. III), 1 mile from Castello [now unknown or destroyed] beyond the Fosso di Rifigliuoli toward S. Quirico" [some 35 km S.E. of Siena].   I think it might be the circled place on the enclosed map, named today "Podere Favorito", or not far from it.'

'The formation "Upper marine clay and lower ocreaceous shale" by Soldani might belong to the formation "P$^{2-1}_{ag}$" in the new edition (1968) (sheet 121) of the official geological map printed by the Italian Geological Survey.   This formation is made by clay, sandy clay, also in continental facies ("Piano del Sentino" Fm.) associated

with small lenses or layers of puddingstone, locally with Lower–Middle Pliocene microfauna.'

Time-stratigraphically, *Batopora clithridiata* (Gregory) from the London Clay (Ypresian) of the London Basin and the forms described by Labracherie (1961, pl. 16, figs 2 and 4) as *Batopora stoliczkai* from the subsurface Lower Eocene of the Bordeaux area, France, vie for the distinction of being the oldest *Batopora* on record. From then onwards the genus occurs in all younger Tertiary stages in Europe (Table 5) with the exception of the Uppermost Miocene. Data are too few, however, to assess whether this absence is fortuitous or indeed reflects the Late Miocene (Messinian) 'Crise de salinité' in the Mediterranean (Hsu, Ryan & Cita, 1972). For more than a century *Batopora* has been considered an extinct genus, until recently one of us found a living representative in the western Indian Ocean, near Zanzibar (Cook, 1966). It appears that *Batopora* had disappeared from western Europe after the Oligocene, and that most Miocene and Pliocene records are from the Mediter-ranean and Parathethys (Map 1, p. 369). In the Pliocene the genus had even ventured out into the western Atlantic. Its present occurrences near Zanzibar and Fiji are curiously remote from the palaeodistribution even in the not-so-distant past, although naturally this may only reflect our ignorance of deeper-water Tertiary faunas from the Indian and the Pacific Oceans.

In contrast to *Batopora*, the genus *Lacrimula* was first described by one of us (P. L. C.) from the Recent, east African coast, and was then found by the other (R. L.) in fossil assemblages from western Europe and the East Indies. Specimens from the Holocene of the northern Indian Ocean have also since been described by Rao & Rao (1973) (see Map 2, p. 370).

Atactoporidra apparently never had a wide distribution, and there are no records after the Oligocene. The three species recorded were from the English and French Eocene, and from the Belgian Eocene and Oligocene.

Conescharellina may have been present in the Eocene of western Europe, although records of species may prove to be referable to *Lacrimula* (see p. 359). The genus seems to have had an almost constant presence in the Australasian region from the late Oligocene to the Recent. (Dr R. Wass, in an unpublished report on stratigraphic ranges of some Bryozoan species from the Tertiary of south-eastern Australia (unpublished report in the Geological Sciences, University of Sydney, 1973 – derived in part from Cockbain, 1971) gives the age of the Mount Gambier fauna as late Oligocene–early Miocene.) *Conescharellina* was common during the Australian Miocene, and there are records from the Pleistocene of the East Indies and Japan. Kataoka (1957) found no *Conescharellina* in a cold-water, Pliocene fauna from Northern Honshu, Japan (approximately 40°N, 140°E). However, by Pleistocene times, probably during an interglacial period, the genus was present further south, at Kikai Jima (approximately 28°N, 130°E, see Kataoka, 1961 : 259). The accompanying large bryozoan fauna included many tropical and subtropical species, including the orbituliporiform *Flabellopora*, and the lunulitiform *Cupuladria* and *Actisecos*. Recent records extend even further north, up to 41°N, 140°E (see Canu & Bassler, 1929b) and west to East Africa (see Map 3 and Appendix 3, pp. 371–373). Generally, the distributions given here may be interpreted as wide, warm water

occurrences during the Eocene and Oligocene, which have either shifted or become progressively restricted in a southerly and easterly direction up to the Recent.

CONCLUSIONS

It has become apparent during this study that the classical concepts both of structure and taxonomy of conescharelliniform colonies require much further work. Analysis of many more samples from additional areas and horizons may begin to throw light upon their evolutionary systematics. At present, we may reach the following conclusions and indicate some of the directions of future research which may prove fruitful.

The overall effects of genetic constitution and environmental selection outweigh microenvironmental effects in colony structure. The conescharelliniform colony has a rigid astogenetic pattern allowing for little variation in the primary zone of change, but allows more in secondary zones, especially in the apical region. Here environmental influences may be the reason for the latitude in astogenetic and ontogenetic expression both within and among populations.

It is possible that convergent lines of evolution with parallel development have occurred, and this possibility requires further investigation.

The obvious physical separation and finiteness of colonies make them very susceptible to statistical analysis of samples. Comparative astogenetic age of colonies within samples is essential. The within-population variation of species requires analysis in the hope of following environmental changes in population characteristics.

Integration within colonies is considerable. A low degree of integration is expressed in colonies where zooids have little interdependence and function in a manner similar to that of solitary animals. Boardman & Cheetham (1973 : 132–134) have suggested several characters with sequences of states showing increasing integration among bryozoan colonies. Using these sequences the wall structure, interzooidal communication, astogenetic zonation and polymorphism of conescharelliniform colonies illustrate a high degree of integration. The devolution of roles among zooids and kenozooids at the earliest astogenetic stages, and the continued development of patterned polymorphs and extrazooidal tissues, are particular examples of colony-wide control.

The specialized mode of life allows palaeoecological inferences to be made as to the depth and nature of the sea-bottom through a considerable range of time.

Future studies on larger samples of more populations should include further examination of type or topotype material of described species. A systematic search of fine-grained sediments, both fossil and Recent, should be made, to enlarge knowledge of distribution and abundance in time and space. Eventually, this should include parallel studies on other orbituliporiform and conescharelliniform species both with 'normal' and 'frontal' astogeny.

A study of similar colony forms such as that exhibited by *Sphaeropora*, which has a Tertiary to Recent range, may throw some light on the evolution of the colony form (see also Waters, 1919 : 80).

The possibility of a study of living colonies may be remote but should not be neglected. The breeding and above all the settlement and early astogeny of a single species would provide guidelines applicable with confidence to other forms.

DESCRIPTIONS OF SPECIES
Family ORBITULIPORIDAE

Orbituliporidae Canu & Bassler, 1923 : 186.

Ascophora with discoidal and bilaminar, or conical colonies, which may be multilaminar. Zooidal calcified frontal wall extensive, cryptocystidean, consisting of two elements, one of which contributes to the exposed surface of the colony and which surrounds a centrally placed orifice. Orifice oval, frequently with paired condyles, occasionally with a distinct antapical sinus. Ovicells usually large, hyperstomial, directed adapically, occasionally immersed. There is constantly a tube, comprising kenozooids and/or extrazooidal tissue, which in some cases extends beyond the colony surface, and which is in contact with the ancestrula or ancestrular complex internally. It is inferred that the tube marks the origin of rootlets which anchored the colony to its substratum. The tube is radially placed in bilaminar (orbituliporiform) colonies, and axially placed in conical (conescharelliniform) colonies. Avicularia and kenozooids often present.

Genus *BATOPORA*

Batopora Reuss, 1867 : 233. Type species *B. stoliczkai* Reuss.

Reuss formally introduced *Batopora* as a new genus, when describing *B. stoliczkai*. Other species were referred to the genus in the discussion, but were not formally described. They included *Cellepora rosula*, which Reuss had described in 1848, and *Conescharellina angustata* d'Orbigny. Waters (1919 : 93) formally listed *B. stoliczkai* as type species of *Batopora*. Canu & Bassler (1917 : 75), however, had already listed '*Batopora rosula* Reuss 1847' as the type species of the genus, which they quoted erroneously as '*Batopora*, Reuss 1847'. This was emended in later works, and Canu & Bassler (1920 : 629) and Bassler (1935 : 54 ; 1953 : G230) gave the type species as *B. stoliczkai*.

Some previous attributions of species to *Batopora* need examination of specimens before they can be assigned to the genus with any confidence. Among these *B. aviculata* Héjjas (1894 : 214, 251, pl. 6, fig. 11) is problematical, and *Batoporella eocaenica* Héjjas (1894 : 215, 252, pl. 7, fig. 13) seems to be related to *Orbitulipora*. Both forms were reported with records of '*B. conica* Hantken' (see p. 359), *B. multiradiata*, *B. rosula* and *B. scrobiculata* from the Eocene of Hungary.

Colony conescharelliniform, with an external or internal adapical tube. Zooids with antapical edge of orifice flattened, peristomes frequently raised, tubular and prominent, exposed frontal walls of zooids often inflated, especially in the proliferal

region.   Avicularia sometimes present, mandibles hinged on a bar.   Ovicells large, hyperstomial but often immersed and obscured by the peristome.   Secondary zones of change formed by frontal budding.   Secondary series of zooids forming overgrowths in some species.

The species previously described in this genus fall into two groups; those in which there are a large number of zooids (maximum seen 200) in a colony, and in which frontal budding of secondary overgrowth is found, and those with a smaller number of zooids (rarely more than 50), in which secondary zooids are irregular in occurrence and in which overgrowth does not occur.

The apical region may be marked by an internal kenozooidal or extrazooidal tube (the 'pit' of authors) or by an external tube.   In some colonies the tube appears to be replaced by a secondarily budded kenozooid.

The first group is represented by *B. multiradiata* and *B. grandis*.   In *B. multiradiata* the colonies often reach a considerable size (3 mm in diameter), and are marked by the development of a distinct type of secondary zone of astogenetic change.   Secondary zooids arise adapically, and apparently form an overgrowth of zooids advancing over the primary zone in a regular manner.   Each zooid is budded frontally from the concealed part of the frontal wall or walls of zooids of the new proliferal region (see p. 326).   This secondary zone is a modified form of overgrowth and thus differs radically both from 'normal astogeny' overgrowth and from frontal budding (see Banta, 1972).   It also differs from the type of secondary zones of change found in *Atactoporidra* and *Lacrimula* (see p. 326).

The secondary zone of change does not always develop regularly, especially during its later astogeny.   Few populations of *B. multiradiata* are well preserved, and wear increases their irregular appearance.   We have been able to examine two well-preserved populations, which show the astogeny both of the primary and secondary zones of change particularly clearly.

Specimens from the Val di Lonte and Montecchio Maggiore (Eocene, Bartonian, Italy, USNM 71205, 7 colonies and 71196, 4 colonies) average 1·25 mm in axial length and 2·75 mm in proliferal region width.   Nearly all these colonies possess a distinct raised apical tube apparently composed of extrazooidal tissue, and surrounded by a circlet of kenozooids.   The secondary astogenetic zone of zooids can be seen to arise in two colonies as a circlet of eight very small zooids just below the tube.   The primary zone consisted of regularly alternating whorls of six zooids. The number in the proliferal zone of secondary zooids varies from 30 to 40 (see Pl. 3, fig. 1 ; Pl. 4, figs 5–6).

Ovicells are present throughout the primary zone and in the last 1–4 whorls of the secondary zone.   They are large, very prominent, and have a regularly pitted surface, which may indicate the presence of pseudopores in life.   Orifices of brooding zooids are wide, with a distinct antapical peristome.   Other colonies from Götzreuth (USNM 88881, Eocene, 65 colonies) may not all belong to *B. multiradiata* but several show clearly that the secondary zone consists of zooids budded frontally in alternating series as an overgrowth of the primary zone (see Pl. 4, fig. 4).   Here, too, ovicells are present in both primary and secondary zones.   These specimens include some very young colonies (see Table 1).

B. grandis also possesses large colonies with numerous zooids. It may produce intercalary rows of zooids, but does not develop a distinct secondary zone of overgrowth.

The second group includes all other known species of *Batopora*. The colonies are never very large, and secondary zones of change are limited to isolated zooids budded frontally from exposed frontal walls of primary zone zooids. This group may be subdivided into species with globular colonies with small zooids (*B. stoliczkai*, *B. clithridiata* and *B. asterizans*) and those with a more conical shape and larger zooids (*B. scrobiculata*, *B. rosula* and *B. murrayi*).

Specimens of *B. stoliczkai* from the Lower Oligocene of Saale (see p. 352), have small colonies with very small zooids and frequently occurring interzooidal kenozooids. Avicularia are absent, but the ovicells are very well preserved and quite prominent. Isolated secondary zooids are fairly frequent in the larger, astogenetically older colonies (see Pl. 1, fig. 1 ; Pl. 2, fig. 2 ; Pl. 3, fig. 4).

B. clithridiata was described as *Conescharellina clithridiata* by Gregory (1893 : 252, pl. 31, figs 10 and 11), from specimens from the London Clay at Sydenham (South London) and Hampstead (North London). The figured colony was separated from a large number from Sydenham (BM 1357) which remained in the Collection under a manuscript name. Nearly all the specimens possess some interzooidal avicularia with a complete bar, many also have small interzooidal kenozooids and isolated secondary zooids (see Pl. 2, fig. 1 ; Pl. 5, fig. 5). *B. clithridiata* has slightly larger zooids than *B. stoliczkai*, in other characters they are very similar.

B. rosula was first described by Reuss (1848 : 78, pl. 9, fig. 17) as *Cellepora rosula*, from the Miocene of Baden, Austria. These specimens have not been examined, but those he described later (1867 : 225, pl. 1, figs 7a–c ; pl. 2, figs 1a–c) have been seen. Reuss apparently illustrated two distinct astogenetic stages of *B. rosula*. Both possess a small, external apical tube, apparently composed of kenozooids, and in both the zooid series were figured as budding directly. The two figured specimens differ in their alternate budding pattern from Reuss's drawings. The remaining three specimens in Reuss's material show a fairly high range of variation. Two of them are irregular in development, and one has a secondarily budded conical kenozooid apically instead of the complex kenozooidal tube of the other colonies. The calcification of the zooids varies from medium to coarsely granular. Generally all five colonies are well preserved and most have ovicells. These are not prominent, and the frontal surface has a distinctly punctate appearance. Axial kenozooids are present in some colonies, and the apical region shows either a small aperture (presumably a pit) surrounded by slightly raised kenozooids or a narrow, raised tube with rows of radially arranged pores on its surface. This tube greatly resembles a zooid in size and shape and seems to be a product of later astogenetic changes in the colony. One colony is worn adapically, and shows traces of the walls of the ancestrular region in section. The primary zooid tetrad surrounds a circular area which presumably marks the position of the apical kenozooid or kenozooidal tube (cf. *B. stoliczkai*, p. 352, and see Pl. 3, figs 2 and 3).

The other Miocene specimens from the Mediterranean area assigned here to *B. rosula* are well within the range of variation shown by Reuss's specimens. The

colonies from Malta and Crete (see Pl. 4, figs 1 and 2) are slightly smaller, and have a secondary kenozooid apically. One specimen from Spain (Roep 1103), which has ovicells, is almost exactly like the colony figured by Reuss (1867, pl. 1, fig. 7).

B. scrobiculata was described by Koschinsky (1885 : 63, pl. 6, figs 2a–c, 3a–c) from the Eocene of Götzreuth. A specimen from this locality (USNM 88882 pt), labelled *B. scrobiculata*, has a flatter colony shape than *B. rosula*, the zooids are very large, comparable with those of *B. grandis* and *B. murrayi*, and easily distinguishable from those of *B. rosula* at a similar astogenetic age. The calcification of the zooids is coarsely granular and axial kenozooids are present (see Pl. 3, figs 5, 6 and 7). The Pliocene *Batopora* from Huelva, Spain, has somewhat similar characters. It has a flattened colony, and the calcification of the large zooids is coarsely granular. In view of its age and locality, it should, however, perhaps be assigned to *B. rosula*.

Batopora stoliczkai Reuss
(Pl. 1, fig. 1 ; Pl. 2, fig. 2 ; Pl. 3, fig. 4)

Batopora stoliczkai Reuss, 1867 : 223, pl. 2, figs 2–4.

MATERIAL EXAMINED. Lower Oligocene, Bünde, Germany, 27 colonies, NMV, 1867.XII, 13a–d. Lower Oligocene, Calbe, Saale, Germany, 5 colonies, USNM.

DESCRIPTION. Colony small, globular. Maximum number of whorls 7. Maximum number of primary zooids in proliferal whorl 3. Maximum number of primary buds 2.

AxL	0·63–0·90 mm	Prl	0·87–1·06 mm
Lfw	0·21–0·23 mm	lfw	0·23–0·25 mm
Lo	0·09–0·10 mm	lo	0·08–0·09 mm
Lov	0·16–0·17 mm	lov	0·18–0·23 mm

REMARKS. The five colonies from Calbe have almost the same characteristics as those from Bünde, except that interzooidal kenozooids are more frequently and regularly developed. The kenozooids do not appear to have any uncalcified central portion, and the small zooid-like structures figured by Reuss (1867, pl. 2, figs 2a, b) as occurring between zooids are thus not exactly as depicted. Among the small kenozooids, the partially closed, half-submerged orifices of primary zone zooids are often visible, below the surface of the secondary zone interzooidal zooids. The antapical axial kenozooids are exactly as figured by Reuss (pl. 2, fig. 3). Of the 32 colonies examined, seven of the specimens from Bünde differ in several ways from the majority. Three colonies are worn, regularly oval in shape and larger than all the others. They appear to have been composed of alternating series, and more than one zone of zooids. The largest colony measures 1·40 mm in axial length and 0·90 mm in proliferal width and comprises approximately 49 zooids. It is very probable that these three colonies are late astogenetic stages of *B. stoliczkai*. Two of the remaining colonies are probably attributable to *Batopora*, but differ from *B. stoliczkai*. They consist of 22 and 30 zooids respectively, arranged in rather irregular whorls of 5–6 zooids each. The colonies are flatter than those of *B.*

stoliczkai (AxL, 0·52–0·64 ; Prl, 1·12–1·30) and have a wide, internal apical tube, surrounded by kenozooids. There are no antapical kenozooids. It is possible that they are representatives of yet another form of *Batopora*, but further specimens would be required to ascertain their specific position.

The two remaining colonies resemble *B. stoliczkai* in zooidal characters, but appear to be at least partially bilaminar. The focus of budding is at the periphery of each colony, from which point alternating zooids are produced facing in opposite directions. These form an astogenetic gradient, becoming larger and more regularly bilaminar so that the colonies form rounded wedges. It is possible that these colonies are very young astogenetic stages of *Orbitulipora*.

Although these last four colonies differ widely from the others, it is just possible that they are variants of *B. stoliczkai* induced by unknown environmental factors, and much more analysis of larger populations would be needed before any further conclusions as to their relationships could be made.

One colony from Bünde shows a very early stage in the astogeny, which may be compared with those described for *Lacrimula asymmetrica* (p. 361). The primary, almost certainly ancestrular, complex consists of a triad of two zooids and a kenozooid. The zooids have elongated peristomes, the kenozooid a wide rounded orifice hardly raised above the remainder of its exposed frontal wall. Two further whorls are present, each consisting of alternating triads of zooids (see Pl. 1, fig. 1). The antapical surface at this stage is flat, and consists of the concealed frontal walls of the last triad only, no kenozooids are present. The next stage present (from Calbe) has 15 zooids and only four whorls of zooids. The four zooids in excess of the estimated number (see p. 333) are secondarily budded zooids arising between those of the first and second whorls. In all larger colonies, secondary buds are more regularly triadic than those in *B. clithridiata*, and tend to be produced in sequence, about one astogenetic generation behind the zooids of the primary zone. The presence of a narrower proliferal region produces the globular appearance of the colonies, which also have a more regular aspect than those of *B. clithridiata* after the 12–14 zooid colony stage, as the small kenozooids are budded between the zooids.

The similarity among young stages of *B. stoliczkai*, *B. murrayi*, and *Trochosodon* sp. is illustrated on Plate 1, figs 1–6.

Batopora grandis[1] sp. nov.

(Pl. 2, figs 5, 6 ; Pl. 3, fig. 8)

HOLOTYPE. Eocene, Götzreuth, Bavaria, BM D31117.

OTHER MATERIAL EXAMINED. Lutecian, Eocene, Götzreuth, Bavaria, with *B. scrobiculata*, *B. multiradiata* and *K. excelsa*, 4 colonies, USNM 88882 ; paratypes.

DESCRIPTION. Colony large, elongated, conical. Maximum number of whorls 12. Maximum number of zooids in proliferal whorl 4. Maximum number of primary buds unknown, probably 4.

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[1] *grandis* – (L) – large – referring to the large size of the zooids.

AxL	1·88–2·72 mm		Prl	1·70–2·00 mm
Lfw	0·40–0·45 mm		lfw	0·35–0·60 mm
Lo	0·14–0·20 mm		lo	0·10–0·12 mm
Lov	0·32–0·50 mm		lov	0·35–0·55 mm

Apical region an internal tube surrounded by small kenozooids. Zooids very large, arranged in directly budded series with secondary zooid series apparently budded regularly between them, forming a spiral pattern. Exposed frontal walls of zooids not inflated, finely granular. Approximately 12 marginal pores in each exposed frontal wall and 8 in each concealed frontal wall. Orifices not raised, apparently with an antapical sinus. Avicularia absent. Ovicells very large, asymmetrically displaced laterally.

REMARKS. The colonies are elongated and very large, and form an astogenetic series. The zooids are very wide and have a spiral arrangement. It is not known whether the orifices are primary or secondary, and most are worn, but some show a distinct and elongated antapical sinus. The apical region consists of a very narrow tube surrounded by 2–3 series of small kenozooids or secondary closed zooids. The number of zooids is very high, especially as there are only four (occasionally an asymmetrically-arranged fifth zooid is present) in the proliferal region. This strongly suggests that the intercalary series of zooids found on the colony surface are budded as in *Lacrimula burrowsi*, which also has a very regular appearance. There is no observable second layer of zooids in the subproliferal region of either of these species, in contrast to *L. similis* and *B. multiradiata*, where the limits of the secondary zone are strikingly obvious.

The ovicells are broken in all specimens and occur on proliferal region zooids only. They are very large, with thick, apparently two-layered walls. Each ovicell is asymmetrical and they resemble those described by Harmer (1957 : 733) in *Conescharellina catella*.

The characters of *B. grandis* are distinct from all other species, but it has features in common with *Lacrimula*, *Atactoporidra* and *Conescharellina*. In size and shape and the possession of an apical tube it resembles *L. burrowsi* and *Atactoporidra bredaniana*. The apparently sinuate orifice and asymmetrical ovicells are superficially, at least, similar to those found in some Recent forms of *Conescharellina*.

B. grandis does not appear to have been described before. It is part of a very interesting fauna of conescharelliniform and similar colonies, all from the Götzreuth locality, which includes *Kionidella*, *B. multiradiata* and *B. scrobiculata*.

Batopora asterizans[1] sp. nov.
(Pl. 2, figs 3 and 4)

HOLOTYPE. Middle Oligocene, 45°95·3′N, 1°31·6′E, North Sea 43/3–1 well, 960–990 ft, BM D52567.

OTHER MATERIAL EXAMINED. As above, 840–870 ft, 3 colonies ; 870–900 ft, 5 colonies ; 1110–1140 ft, 1 colony ; 1530–1560 ft, 1 colony ; paratypes. Rupelian,

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[1] *aster* – (L) – a star – referring to the stellate appearance of the apical and axial kenozooids.

probably Middle Oligocene, Ijzendijke, Zeeland, boring K62, Boom Clay, 5 colonies ; paratypes.

DESCRIPTION. Colony small, conical to globular. Maximum number of whorls 6. Maximum number of zooids in proliferal whorl 3. Maximum number of primary buds 3.

AxL	0·70–0·75 mm	Prl	0·90–1·00 mm
Lfw	0·20–0·25 mm	lfw	0·25 mm
Lo	0·06–0·09 mm	lo	0·07–0·09 mm

Apical region apparently consisting of a secondarily budded kenozooid. Zooids arranged in alternating series, with small globular kenozooids arising interzooidally and usually alternating with the zooids. Circles of apical kenozooids and a group of axial, antapical kenozooids present. Frontal walls of zooids distinctly, almost coarsely granular. Exposed frontal walls inflated, with six marginal pores. Primary orifices not seen, secondary orifices oval. Ovicells and avicularia not seen.

The apical region is marked by an inner circle of five, and an outer circle of eight, alternating, globular kenozooids (diameter 0·14 mm). These presumably have over-grown the primary zooids, and also occur, budded interzooidally, fairly regularly in alternating series among the zooids. A further, axial group of five kenozooids is also present.

REMARKS. *B. asterizans* has a similar growth form to that of *B. stoliczkai* and *B. clithridiata*. The arrangement of the zooids and alternating kenozooids is, however, much more regular than in either of these species. It further differs from *B. clithridiata* in the absence of avicularia.

The colonies are all very small and none have ovicells. It is therefore possible that larger colonies may eventually be found, although ovicells occur in both *B. stoliczkai* and *Trochosodon* (see Pl. 1, figs 5 and 6 ; Pl. 2, fig. 2) in colonies of comparable size to those of *B. asterizans*. Generally the colonies are regularly constructed, although one from the North Sea shows several frontally budded secondary interzooidal zooids which results in an appearance very similar to that of *B. clithridiata*.

The apical tube is raised and appears to consist of a secondarily budded kenozooid. It is regularly surrounded by small, rounded kenozooids, which are inferred to be secondarily budded, as one very small colony from the North Sea shows only three kenozooids, whereas larger examples show two series of 5–8 kenozooids.

Genus *LACRIMULA*

Lacrimula Cook, 1966 : 217. Type species *L. burrowsi* Cook.

Colony conescharelliniform, with an external tube. Zooids with rounded orifices, and often well-developed paired condyles, sinus occasionally present. Interzooidal avicularia sometimes present. Ovicells large, hyperstomial, prominent. Secondary zone of frontal buds arising directly from exposed frontal walls of primary zone zooids, beginning adapically.

Specimens ascribed here to *Lacrimula* vary from small elongated colonies which have some morphological affinity to the *Batopora rosula* group (*L. borealis*) to complex colonies with well-developed zones of secondary zooids which approach, superficially at least, those of *Atactoporidra bredaniana* and *Batopora multiradiata*.

Some species also show an interesting similarity in character with *Conescharellina*. Both *L. visakhensis* and *L. perfecta* possess regular axial series of kenozooids, and *L. visakhensis* resembles *C. africana* in producing adapical ovicells.

Generally *Lacrimula* includes species in which the colony is elongated and the apical region consists of a prominent kenozooidal tube.

Lacrimula burrowsi Cook

(Pl. 5, figs 1, 6 ; Pl. 6, fig. 3 ; Pl. 8, figs 1–6)

Lacrimula burrowsi Cook, 1966 : 218, pl. 2, figs 2–4 ; fig. 4A.

MATERIAL EXAMINED. Recent, Zanzibar, 101 m, 207 m, 37 colonies, BM John Murray Coll. 1965.8.24.7–10, 1965.8.24.11 ; paratypes. Off Umvoti River, S. Africa, 102 m, 34 colonies, BM Burrows Coll., 1949.11.10.642.

DESCRIPTION. Colony elongated, often slightly flattened in one direction. Maximum number of whorls 19. Maximum number of zooids in proliferal whorl 6. Maximum number of primary buds 6.

AxL	2·00–3·20 mm	Prl	1·24–1·88 mm
Lfw	0·30–0·37 mm	lfw	0·30–0·45 mm
Lo	0·10–0·15 mm	lo	0·10–0·11 mm
Lov	0·14–0·30 mm	lov	0·15–0·17 mm

Apical region a tube with closely spaced external pores. Zooids primarily budded in alternating series, with avicularia frequently, but often irregularly interspersed. Frontal wall of zooids finely granular. Exposed part of frontal wall with 4–6 marginal pores, 4–6 pores in concealed part. Primary orifice divided at the mid-line by large condyles. Ovicells large, occurring in the proliferal and subproliferal zone zooids. Fertile orifices not dimorphic, closed by the operculum. Avicularia arising as frontal buds between adjacent primary zooids. Chamber large, but not reaching the axial region of the colony. Exposed part of frontal wall of chamber with marginal pores. Semicircular mandible hinged to large, paired condyles. Rostra directed adapically and slightly laterally, sometimes alternating in radial series.

The first whorl of individuals below the apical region consists of avicularia ; these are secondary in origin. Secondary calcification affects zooids progressively from the apical region in an antapical direction. In some colonies the first seven whorls are comprised of zooids with closed orifices, which may have a small central rounded opening.

REMARKS. A large number of colonies of *Lacrimula burrowsi* have recently been found in bottom sediment samples kept by the Mineralogy Department of the British Museum (Natural History). The samples were all from the Zanzibar area and were collected by the John Murray Expedition to the Indian Ocean. The colonies were

dried and were therefore restored in trisodium phosphate solution and stained before being mounted in epoxy-resin and sectioned. These sections have shown details which generally support some of the inferences about colony structure suggested here.

The marginal pores appear in longitudinal section as small tubules, often filled with stained tissue, passing through the thick calcification of the concealed frontal wall of one zooid into the living chamber of the next successive zooid. Tubules tend to be concentrated towards the axial end of zooids (see Pl. 8, figs 1 and 2). They are very similar in appearance to the extended 'areolar' tubules, which are derived from frontal septulae, in other Bryozoa.

The apical region shows the ancestrular whorl of zooids to be surrounded by very thick calcification. A series of large tubular pores, each surrounded by calcification, forms the apical tube (see Pl. 8, fig. 5). The pores are inferred to be the coelomic cavities of kenozooids ; they are often filled with stained tissue and pass from the exterior of the apical tube into a large interior cavity. This cavity is lined with stained tissue and it is inferred from analogy with the marginal pore tubules that neither the axial kenozooid nor the smaller kenozooids forming the tube had any connection directly with the exterior environment in life, but may have been the site of rootlets. Although elongated tubules extend from the primary zooids to the secondarily budded avicularian chambers at the base of the kenozooidal tube, there does not appear to be any communication among the small kenozooids. If the axial cavity marks the position of the coelomic cavity of a kenozooid, the smaller cavities would have been able to intercommunicate. Generally, all these structures need much more work, in this and other species, particularly those which can be demonstrated to have rootlets. The apical structures in *L. burrowsi*, however, appear to be consistent with the postulate that they were the site of rootlets arising from highly modified kenozooids which were budded successively in an adapical direction from a large axial kenozooid.

Lacrimula visakhensis Rao & Rao
(Pl. 6, fig. 4)

Lacrimula visakhensis Rao & Rao, 1973 : 506, fig. 1.

MATERIAL EXAMINED. Holocene, Bay of Bengal, E. India, 89 m, 4 colonies, BM Subba Rao Coll. 1970.8.8.1 A–D.

DESCRIPTION. Colony small, conical. Maximum number of whorls 7. Maximum number of zooids in proliferal whorl 8. Maximum number of primary buds 8.

AxL	1·12–2·20 mm	Prl	1·60–2·00 mm
Lfw	0·23–0·25 mm	lfw	0·25–0·40 mm
Lo	0·12–0·18 mm	lo	0·10–0·16 mm
Lov	0·25–0·32 mm	lov	0·30–0·40 mm

Apical region a tube with large external pores. Primary zooids budded in direct series. Secondarily budded series of zooids confined to the adapical end of the zoarium. Axial region composed of small kenozooids. Frontal wall of zooids very

finely granular.   Marginal pores 2–6 in exposed part of frontal wall, 8–11 in concealed part.   Primary orifice oval, divided adapically to the mid-line by small, paired condyles.   Both adapical and antapical parts curved ; peristome absent. Ovicells very large and wide, orifice wider than long.   Brooding zooids budded secondarily from zooids at the adapical end of the colony.   Frontal surface of ovicell granular, marginal pores present.   Avicularia arising as frontal buds between adjacent zooids in the adapical region ; mandibles inferred to have been rounded. Avicularia are not common, occurring laterally beside a zooidal orifice in a few zooids only ; they have no bar or condyles and are inferred to be avicularia only by their size and position.

The first whorl of zooids in the young colony is hidden by a whorl of avicularia which are budded between the primary zooids.

REMARKS.   The condyles of the autozooidal orifices are placed distinctly adapic-ally, those of brooding zooids are not visible.   The ovicells occur in a single whorl at the adapical end of the colony, and all arise as secondary zooid buds between primary zooids.

Antapically the concealed frontal walls of the youngest proliferal region zooids show that the marginal pores do not extend axially to the limit of each zooid.   They form a row half-way across the wall.   The axial region is filled with 6–8 very small kenozooids.

L. visakhensis differs from other species of *Lacrimula* in the position of the con-dyles, and in the astogeny, position and frontal wall characteristics of the ovicells. It resembles *L. perfecta* in possessing axial kenozooids, and *Conescharellina africana* in the apical position of the ovicells.

Lacrimula perfecta (Accordi)

(FIG. 7A ; Pl. 4, fig. 3 ; Pl. 7, fig. 1)

Conescharellina perfecta Accordi, 1947 : 105, figs 1–7 ; Braga & Munari, 1972.

MATERIAL EXAMINED.   Priabonian, Upper Eocene, Cunial Quarry, Possagno, N. Italy, 16 colonies and several fragments, collected by Drs E. Annoscia and P. Ascoli, 1968.   Priabonian, Upper Eocene, Forte di San Leonardo, Verona, N. Italy, 31 colonies, collected by Dr G. Braga.

DESCRIPTION.   Colony conical to pyriform.   Maximum number of whorls 20. Maximum number of zooids in proliferal whorl 9.   Maximum number of primary buds 6.

AxL	0·75–3·40 mm	Prl	0·86–2·80 mm
Lfw	0·19–0·40 mm	lfw	0·20–0·45 mm
Lo	0·09–0·12 mm	lo	0·09–0·14 mm
Lov	0·17–0·20 mm	lov	0·25–0·30 mm

Colony with a distinct kenozooidal apical tube with external and internal un-calcified pores.   Tube becoming very large, bulbous and thick by accretion of kenozooids during astogeny (1·00 mm in diameter), with a very small central

aperture at the apex (0·10 mm in diameter).   Axial kenozooids also budded regularly in series forming a central core (1·60 mm in diameter).   Zooids with a non-sinuate orifice, wider antapically, with paired lateral condyles.   Zooids budded in alternating series ; later, intercalary series also budded.   Avicularia small, regularly budded between two orifices, oval with a complete bar, mandible directed laterally.   Ovicells present in larger colonies, fairly prominent and globular.

REMARKS.   The attribution of this form to *Conescharellina* in the past was dependent on the possession of regularly patterned avicularia and axial kenozooids.   Both these characteristics now appear not to be exclusive to *Conescharellina*.   Regularly patterned avicularia also occur in *L. grunaui* and in many colonies of *L. burrowsi*, although in both this last species and *L. perfecta* there are colonies in which the occurrence and distribution of avicularia are much less regular.   Axial kenozooids are present in *L. visakhensis*, *L. similis* and *L. perfecta*.   The general distinction between the two genera has thus become progressively restricted to the nature of the primary orifice and, to a lesser extent, to the nature of the apical region of the colony.

Sinuate orifices occur in *L. asymmetrica* and *L. grunaui*, but do not have the very distinct, narrow sinus usually associated with species of *Conescharellina*.   All other species assigned to *Lacrimula* have rather large, non-sinuate orifices, which tend to be wider rather than narrower antapically.   The apical region in *Lacrimula* is typically formed by a kenozooidal tube ; that in *Conescharellina* by kenozooids, avicularia and 'lunoecia' (rootlet pores).   Forms of *Conescharellina* from E. Africa (*C. africana* and an unnamed species of *Conescharellina*, see Appendix 3, p. 372), apparently have no rootlet pores.   *C. africana* has an accumulation of kenozooids, ringed by avicularia, but no axial aperture (see Cook, 1966 : 215).   The other species of *Conescharellina* has a small but distinct kenozooidal tube apically.

The correlation of apical region with orifice shape, although not exclusive, has decided the attribution of *C. perfecta* to *Lacrimula*.

Accordi (1947 : 108, figs 8–10) also described another form, *C. veronensis*, from the same Italian deposits.   An analysis of further samples from the area was made recently by Braga & Munari (1972), who concluded that *C. veronensis* was a synonym of *C. perfecta*.

The nature of the larger Upper Eocene specimens does, however, raise another problem.   A species with a conescharelliniform colony was described as *C. eocoena* by Neviani (1895 : 122, fig.) from the Eocene of Mosciano, near Firenze.   Only one specimen was found and that was not well preserved.   Its principal characters were rounded orifices and, possibly, small avicularia between zooids ('piccolo aperture vibracolifere (?) sul solco superficiale che divide i vari zoeci').   The colony had an axial length of 2·33 mm, and a proliferal width of 1·47 mm.   Neviani considered that *C. eocoena* was close to '*Batopora conica* Seguenza (non Hantken)' which had been described and figured earlier in very similar terms (see Seguenza, 1880 : 42, pl. 4, fig. 10).   Seguenza's specimens were from the Tongrian (Oligocene) of Antonimina, Reggio Calabria.   Waters (1921 : 424) regarded Neviani's, Seguenza's and Hantken's species as synonymous, but pointed out that '*B. conica* Hantken' was almost certainly a manuscript name.

The lack of well-preserved type specimens for examination, together with the nomenclatural confusion inherent in using Seguenza's name, which antedates that of the Recent form, *C. conica* Haswell (1880 : 42, pl. 3, figs 7 and 8), suggests that, for the present at least, the name used for his Eocene record should be *C. eocoena* Neviani. Specimens in the British Museum, Palaeontology Department, labelled '*Batopora conica* Hantken' from the Hantken Collection (B3724 Buda, Szaboi beds, Lower Clay, Eocene) were mentioned by Waters (1921 : 424). These colonies are very large (AxL 4·00–6·50 mm, Prl 3·50–4·00 mm) and very worn. Their appearance is, however, similar to that of the far better preserved large specimens of *L. perfecta* from San Leonardo. The orifices are rounded, and there are small pores between them placed regularly as are the avicularia in *L. perfecta*. Series of axial kenozooids are present, and the bulbous apical region (diameter 2·00 mm) has a very small central aperture. These colonies are associated with many other, mainly erect species of Bryozoa, and with *Lunulites* and *B. multiradiata*.

It thus appears possible that some, perhaps all, fossil records of *Conescharellina* from western Europe may prove to belong to one species-complex, attributable to *Lacrimula*.

Lacrimula borealis[1] sp. nov.

(Pl. 7, figs 4, 5)

HOLOTYPE. Middle Oligocene, 45°95·3′N, 1°31·6′E,. North Sea 43/3–1 well, 1430–1470 ft, BM D52568.

OTHER MATERIAL EXAMINED. As above, 840–870 ft, 1 colony ; 1860–1890 ft, 1 colony ; paratypes.

DESCRIPTION. Colony small, conical. Maximum number of whorls 6. Maximum number of zooids in proliferal whorl 3. Maximum number of primary buds 3.

AxL	0·50–1·20 mm	Prl	0·90–1·15 mm
Lfw	0·38–0·50 mm	lfw	0·40–0·55 mm
Lo	0·16–0·22 mm	lo	0·15–0·17 mm
Lt	0·28–0·50 mm		

Apical region a long narrow, prominent tube with granular calcification and occasional pores. Zooids large, with frontal wall very slightly inflated, with 6–8 marginal pores. Peristome absent, primary orifice large, rounded adapically, straight antapically, apparently without condyles. Avicularia and ovicells not seen (see below).

REMARKS. The colonies are obviously at a very early astogenetic stage, but the zooids are very large in comparison with other species of comparable age. The kenozooidal tube is long, with 4–8 regularly spaced pores on its outer surface, and a very small apical aperture.

Each of the three colonies includes one peripheral zooid which has a small, rounded foramen (approximately 0·07 mm in diameter) in the wall adapical to the orifice

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[1] *borealis* – (L) – northern – referring to the distribution of the species.

(see Pl. 7, fig. 5). The cavity behind the foramen does not appear to be confluent with the zooid living chamber. By analogy with other species, this would therefore appear not to be a brooding zooid with adapical ovicell. The lack of other structures such as condyles, etc., also make it unlikely to be an avicularium, and as the chamber is apparently part of a zooid, it cannot be interpreted as a kenozooid. Until more specimens can be found, the nature and possible function of these distinctive structures is unknown.

Lacrimula asymmetrica[1] sp. nov.
(Fig. 6 ; Pl. 5, fig. 4 ; Pl. 7, fig. 3)

HOLOTYPE. Miocene, 07°00'S, 113°00'E, Kombangan, W. Madura, Indonesia, Tertiary f¹, *Globigerinatella insueta* zone (see van der Vlerk & Postuma, 1967, fig. 1), BG 312, BM D52569.

OTHER MATERIAL EXAMINED. As above, 39 colonies ; paratypes.

DESCRIPTION. Colony pyriform, asymmetrical. Maximum number of whorls 7. Maximum number of zooids in proliferal whorl 4–5 alternating. Maximum number of primary buds 1 + 4.

AxL	0·55–1·50 mm	.	Prl	0·42–0·88 mm
Lfw	0·17–0·25 mm		lfw	0·15–0·25 mm
Lo	0·08–0·13 mm		lo	0·05–0·10 mm
Lt	0·15–0·30 mm			

Apical region a tube, with closely spaced, small external pores. Whorls of zooids alternate in number from 4 to 5 so that the whorls are only approximately arranged in a plane perpendicular to the colony axis, and the outline is asymmetrical. Secondary frontal buds forming a secondary zone of change are first produced at the adapical end of the colony. Frontal walls of zooids very finely granular and apparently non-porous, except for occasional marginal pores. Primary orifices of primary zooids with a very narrow adapical shelf which terminates abruptly to form paired condyles. Adapical part of the orifice sub-circular, the antapical part rounded-triangular, slightly narrower. No peristome present. Primary orifice of secondarily budded zooids ovate, apparently without condyles. Ovicells and avicularia not observed.

REMARKS. Secondary calcification has affected at least two whorls below the apical region, completely closing the orifices, or leaving a semi-lunar slit. The specimens of *L. asymmetrica* comprise an almost complete astogenetic series, from the early stage of one whorl of zooids to the development of the secondary zone of astogenetic change.

The earliest stage present has only five zooids. The colony measures 0·45 mm in axial length and 0·40 mm in proliferal region width. Among these zooids there is one, which may have been slightly earlier in development than the others, slightly asymmetrical in position. The ancestrular region is completed by an apical, axial

[1] *asymmetros* – (G) – asymmetrical – referring to the shape of the colony.
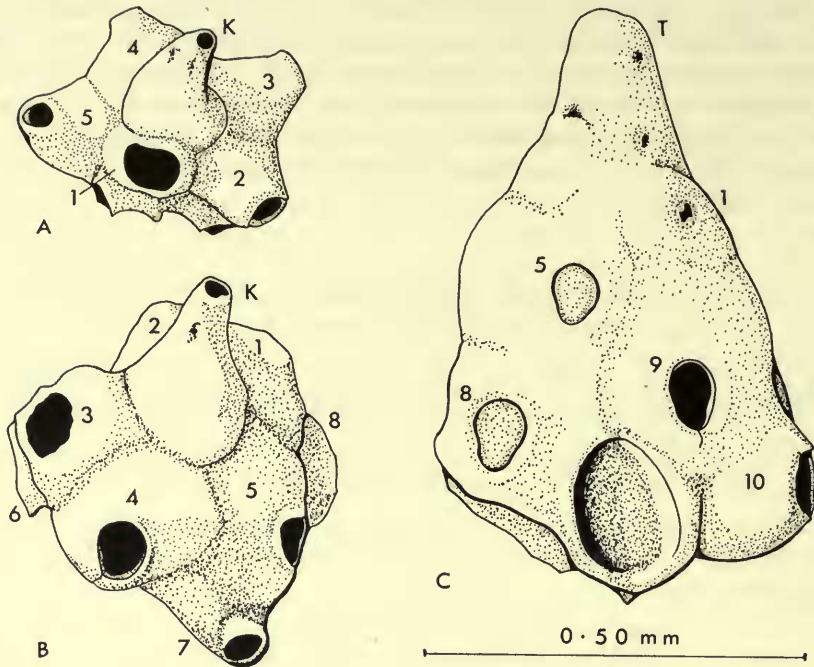
24

FIG. 6.   Early astogenetic stages in *Lacrimula asymmetrica* sp. nov.
   A. Colony comprising apical kenozooid and first whorl of 5 zooids (1 is asymmetrically developed).   This colony has slightly smaller zooids than those of others at the same stage.   K, kenozooid.
   B. Colony comprising apical kenozooid, first whorl of 5 and second whorl of 4 zooids. K, kenozooid.
   C. Colony comprising apical kenozooidal tube, enlarged by astogenetic development of kenozooids, or by ontogenetic thickening of primary tube, or by extrazooidal tissue, or a combination of any or all methods.   Note three whorls of zooids present (5, 4, 5), total 14 ; the first whorl zooid orifices are occluded.   T, apical kenozooidal tube.

elongated kenozooid, its tube extending 0·15 mm above the colony surface.   Other young colonies show slight variations on this theme, but it is interesting that the alternating whorls of 4–5 zooids are present in the earliest stages, as is the kenozooidal tube, which in some cases reaches 0·20 mm in length at this stage.   Later development consists of the budding of further alternating whorls and of the appearance of rugosities and pores on the surface of the kenozooidal tube, which becomes both thicker and longer.   It is not known whether this is the result of kenozooidal budding, growth of extrazooidal tissues or both.   By the time the colony has reached a size of 1·50 × 0·50 mm, and comprises 18 zooids, the tube may be 0·30 mm in length and may have expanded to a width of nearly 0·20 mm and be covered by 15–20 pores or depressions.   The first whorl of orifices is often closed by calcification at this stage, and appears to have become incorporated into the calcification of the kenozooidal tube.   At this stage, or even earlier, growth of the secondary zone begins.   It starts with the production of frontal buds almost simultaneously

from the second and third zooid whorls and extends, apparently fairly rapidly, to the remaining whorls.   The primary zooids may also produce frontal buds, but at a slightly later stage.   Some, but not all, of the primary zooids may have orifices closed by calcification when the buds are produced ; in others the orifices of the primary zone zooids may be seen through the orifice of the secondary zooid.

Lacrimula grunaui[1] sp. nov.
(FIG. 7B ; Pl. 7, fig. 2)

HOLOTYPE.   Miocene, 07°00′S, 114°00′E, Batuputih, E. Madura, Indonesia, Tertiary f[1], *Globigerinatella insueta* zone (see van der Vlerk & Postuma, 1967, fig. 1), G 5671, BM D52570.

OTHER MATERIAL EXAMINED.   As above, 6 colonies ; paratypes.

DESCRIPTION.   Colony elongated, pyriform, slender. Maximum number of whorls 10.   Maximum number of zooids in proliferal whorl 4.   Maximum number of primary buds 4.

AxL	0·81–1·60 mm	Prl	0·70–0·88 mm
Lfw	0·20–0·25 mm	lfw	0·20–0·25 mm
Lo	0·11–0·13 mm	lo	0·07–0·10 mm
Lt	0·10–0·20 mm		

Apical region a tube, with closely spaced, small external pores.   Each zooid with a consistently placed antapical avicularium.   Frontal walls of zooids very finely granular, apparently non-porous, except for occasional marginal pores.   Primary orifice with distinct, paired condyles, which separate a sub-circular adapical portion from a large, semicircular but narrower antapical part.   No protruding peristome present, but the adapical side of the orifice is slightly raised.   Ovicells not observed. Avicularian chambers situated adjacent to the central part of the concealed frontal wall, not reaching the colony axis.   Exposed part of avicularian chamber very small, triangular, with a delicate cross-bar, the rostrum rounded-triangular and antapically directed.

The orifices increase rapidly in size (1·5 times in 5 whorls).   Secondary calcification affects the first two whorls below the apical region.   It has almost closed the orifices, leaving a vertical slit.

REMARKS.   *L. grunaui* differs from *L. asymmetrica* in the very symmetrical growth of the zooid whorls, and in the possession of avicularia.

Lacrimula similis[2] sp. nov.
(FIG. 7C ; Pl. 6, figs 1, 2)

HOLOTYPE.   Miocene, 07°00′S, 113°00′E, Kombangan, W. Madura, Indonesia, Tertiary f[1], *Globigerinatella insueta* zone (see van der Vlerk & Postuma, 1967, fig. 1), BG 312, BM D52571.

[1] Named for Dr H. R. Grunau, who collected the specimens.
[2] *similis* – (L) – resembling – referring to the similarities of this species with both *L. grunaui* and *Conescharellina*.
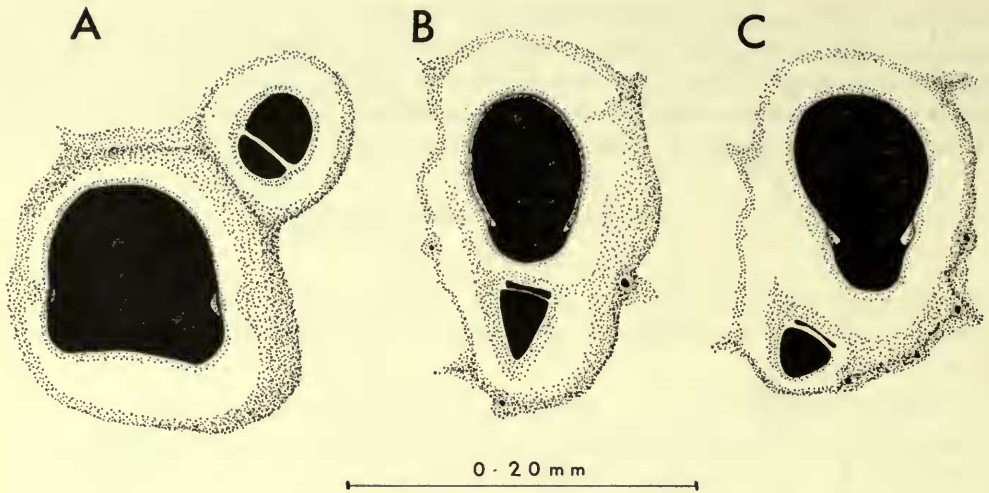
FIG. 7.   Orifice and interzooidal avicularium in *Lacrimula*.   A. *L. perfecta*.
B. *L. grunaui*.   C. *L. similis*.   Scale = 0·20 mm.

OTHER MATERIAL EXAMINED.   As above, 12 colonies ; paratypes.

DESCRIPTION.   Colony conical, irregular.   Maximum number of whorls (secondary zone) 10.   Maximum number of zooids in primary proliferal whorl 4.   Maximum number of zooids in secondary proliferal whorl 10.   Maximum number of primary buds 4.

AxL	1·16–1·36 mm	Prl	1·20–1·44 mm
Lfw	0·25–0·26 mm	lfw	0·25–0·26 mm
Lo	0·12–0·14 mm	lo	0·08–0·12 mm
Lt	0·08–0·15 mm		

Apical region originally a short tube, later surrounded by secondary and tertiary zone zooids and transformed into a shallow pit.   Zooids budded in alternate series. Frontal wall smooth.   Primary orifice with minute condyles, delimiting a distinct antapical sinus.   Avicularia arising as frontal buds, placed asymmetrically on one side of the antapical part of the orifice which is raised as a peristome.   Avicularian rostrum rounded, with a complete bar, directed laterally and antapically.   Subrostral chamber large.   Ovicells not seen.   Small, rounded axial kenozooids formed late in astogeny.

REMARKS.   The size and position of the avicularia distinguish this species from *L. grunaui*, to which it appears to be closely related.   It also differs in the very early development of secondary and even tertiary zones of change, neither of which has been found in colonies of *L. grunaui* of similar size and astogenetic age.   The primary zone of change apparently consists of whorls of four zooids, but as few as three to four whorls are present when the secondary zone of change appears.   It begins as a series of small buds arising apically and surrounding the small, shallow kenozooidal

tube. The secondary zone consists of zooids budded directly frontally from primary zooids and is not an overgrowth. Primary zone orifices may be seen through those of secondary zone zooids as in *L. asymmetrica*. The zone is very regular, a complete whorl being budded simultaneously and the sequence is in an antapical direction. Superficially, the colonies may resemble those of *B. multiradiata* as the secondary zone zooids advance on a front over those of the primary zone. In some colonies a third zone arises antapically. The avicularia are enlarged in comparison to the zooids and seem to form a special group comparable with those found in *Conescharellina africana* (see Cook, 1966). In fact, *L. similis* superficially resembles some species of *Conescharellina* with its adapical avicularia and sinuate orifices. It also develops axial antapical kenozooids which cover the concealed frontal walls of the proliferal region zooids.

Genus *ATACTOPORIDRA*

Atactoporidra Canu & Bassler, 1931 : 22 ; new name for *Atactopora* Canu & Bassler, 1929b : 50 (preoccupied). Type species *Atactopora bredaniana* (Morren).

Canu & Bassler placed this genus in the Orbituliporidae and described the colony as 'libre'. Their generic description described the zooids as 'amoncelées en désordre les unes sur les autres'. Additional information is now available as to the character of the genus, and the description has therefore been somewhat modified.

Colony conescharelliniform, with an apical kenozooidal tube. Primary zooids budded in alternating series. Secondary to quaternary series of zooids budded concurrently with the later zooids of the primary series, originating from the exposed frontal walls of the primary zone zooids, either directly or in alternating series.

Three species of *Atactoporidra* have been described, *A. bredaniana*, *A. glandiformis* and, more recently, *A. globosa* (see Labracherie, 1961). *A. glandiformis* was discussed by Cheetham (1966 : 106, fig. 81). In this species there seems to be an actual increase in the number of zooid series in the primary zone, as well as an increase in size. Similarly budded series of zooids arise antapically quite early in the astogeny, but the apical region is rarely affected.

Atactoporidra bredaniana (Morren)

(Pl. 5, fig. 2 ; Pl. 6, fig. 6)

Atactopora bredaniana (Morren) Canu & Bassler, 1929b : 51, pl. 4, figs 1–6.
Atactoporidra bredaniana (Morren) Canu & Bassler, 1931 : 22, pl. 4, figs 5 and 6 ; Dartevelle, 1933 : 85, 108.

MATERIAL EXAMINED. Eocene, Wemmel sands, Laeken, Belgium, 4 colonies, BM Dartevelle Coll., D33249–59. ? Eocene, Belgium, 20.11.1905, 50 colonies, BM Vassall Coll., D7864.

DESCRIPTION. Colony elongated, pyriform, irregular. Maximum number of whorls 22. Maximum number of zooids in proliferal whorl 6. Maximum number of primary buds 4.

AxL	2·20–4·60 mm	Prl	0·80–1·20 mm
Lfw	0·30–0·35 mm	lfw	0·30–0·32 mm
Lo	0·13–0·16 mm	lo	0·10–0·11 mm
Lov	0·14–0·16 mm	lov	0·15–0·17 mm
Lt	0·15–0·30 mm		

Apical region with a short tube with external pits and ridges of calcification. Frontal wall of zooids finely granular, marginal pores not seen. Primary and secondary zooidal orifices apparently without condyles. Ovicells hyperstomial, prominent, associated with tertiary and quaternary zooidal series. Avicularia not budded frontally. At the sides of the raised peristomes of some ovicelled zooids, there is a small pore, which is inferred to have been an adventitious avicularium.

REMARKS. The four specimens previously examined by Cook (1966 : 217) are worn, and had developed several series of secondarily frontally budded zooids before preservation. The basic structure of the colony was therefore not readily apparent. Examination of the more plentiful, astogenetically younger, and better preserved material from the Vassal Coll. not only enables the astogeny of the colony to be inferred but shows that *Atactoporidra* and *Lacrimula* have many more characters in common than was first realized.

The specimens (D7864) include colonies in which the irregular series of secondary buds are not much developed, and in which a distinct apical kenozooidal tube is present. The arrangement of the primary zooids is regular and alternating. The orifices of the zooids are small, rounded adapically and nearly straight antapically. The ovicells have been seen in a few specimens only, and all have broken frontal walls. They are present only on the tertiary to quaternary zooidal series, are randomly placed and irregularly orientated.

The greatest concentration of secondary to quaternary frontal budding is in the antapical part of the colony, causing irregularity of outline and a confused appearance of the surface. The budding apparently occurs at the apical end of the colony at a late astogenetic stage. No progressive closure of zooidal orifices from the apical end has been seen as in *Lacrimula*. Secondary zooidal series appear to arise directly from the exposed frontal walls of primary zooids, but tertiary and quaternary series often arise alternately between zooids of the secondary series, and their orientation is irregular.

One colony of *A. bredaniana* from D7864 is rod-shaped and measures 3·00 mm long by 1·00–1·20 mm wide. The zooids of the primary zone of change are visible adapically. Secondary zooids comprise the antapical part of the colony, which is hardly wider than the adapical part. Some colonies may therefore show very little increase in size of zooids in the primary zone of change. It is not possible to see whether a primary zone of repetition occurred.

Dartevelle (1933) reported *A. bredaniana* not only from the Wemmel sands (Bartonian) but from the earlier Lédien ('gravier de base, sables à *N. variolarius*')

which he equated with the Upper Bracklesham of England. Many other bryozoan species, including *Lunulites*, were present.

SUMMARIES IN FRENCH AND GERMAN

Les colonies conescharelliniformes et orbituliporiformes de Bryozoaires, et l'occurrence dans les deux groupes de deux formes de bourgeonnement, le 'normal' et le 'frontal', sont décrits. Les genres *Conescharellina* et *Trochosodon* sont connus d'être fixés aux leurs substrata par les petits racines. Ils sont comparés avec les genres *Batopora*, *Lacrimula* et *Atactoporidra*. On suggère un modèle hypothétique pour la croissance primaire de la colonie dans ces genres. Les caractères et le distribution dans le temps et dans l'espace de genres *Batopora*, *Lacrimula*, *Atactoporidra* et *Conescharellina* sont discutés, et on enregistre l'information à l'égard de leur

écologie et leur paléoécologie. Les descriptions complètes sont donnés de trois espèces de *Batopora*, dont deux espèces sont considerées d'être nouvelles, et de sept espèces de *Lacrimula*, dont quatre espèces sont considerées d'être nouvelles. Les efforts combinés de génétique et d'environnement surpassent les influences micro-environmentales dans les limites de la colonie. L'intégration dans les colonies même est considérable, elle est démontrée par les communications interzooidales, la zonation astogénétique et le polymorphisme. La manière de vivre particulière permets que les conclusions paléoécologiques soient faites quant à la profondeur et le type du fond de la mer, depuis le Eocène jusqu'au Récent.

Conescharelliniforme und orbituliporiforme Kolonien von Bryozoen und das Auftreten von zwei Typen von Astogenie, 'normaler' und 'frontaler', in beiden Gruppen werden beschrieben. Die Gattungen *Conescharellina* und *Trochosodon*, die durch Würzelchen mit ihrem Substrat verankert sind, werden mit den Gattungen *Batopora*, *Lacrimula* und *Atactoporidra* verglichen. Ein hypothetisches Modell für die Anfangsentwicklung der Kolonien dieser Gattungen wird vorgeschlagen. Die Merkmale und die zeitliche und räumliche Verbreitung der Gattungen *Batopora*, *Lacrimula*, *Atactoporidra* und *Conescharellina* werden diskutiert und die verfügbaren Daten über ihre Ökologie und Paläo-Ökologie werden angeführt. Drei Arten der Gattung *Batopora*, zwei davon neu, und sieben Arten der Gattung *Lacrimula*, vier davon neu, sind ausführlich beschrieben. Der kombinierte Einfluss von Genetik und Umwelt überwiegt die Mikroeinflüsse innerhalb der Kolonie. Integration innerhalb der Kolonien ist beträchtlich und drückt sich aus in interzooidaler Kommunikation, astogenetischer Zonenbildung und Polymorphismus. Die spezialisierte Lebensweise gestattet paläo-ökologische Schlüsse über die Tiefe und Beschaffenheit des Meeresbodens vom Eozän bis zur Jetztzeit.

APPENDICES

Appendix 1

The following records of *Batopora* have been plotted on Map 1. Many records include more than one species ; previously unpublished observations are noted thus '(R. L. obs.)'.

RECENT. Zanzibar, 805 m (Cook, 1966) : *B. murrayi*.
　　Fiji, Challenger Stn 174D, 384 m (P. L. C. obs.) : *B. murrayi*.

PLIOCENE. Sassuolo, near Modena, Italy (Namias, 1891) : *B. rosula*.
　　Huelva–1 well, near Huelva, Spain, 648 m (ditch cuttings) (R. L. obs.) : *B. rosula*.

MIOCENE. Crete, Sample 6–27, Almiri section (R. L. obs.) : *B. rosula*.
　　Malta, Sample PLR 4067, Blue Clay Formation (R. L. obs.) : *Batopora* sp.
　　Arzeboun II, Prov. du Mäzänderan, Iran (Dartevelle, 1948) : *B. ernii*.
　　Benestare, Calabria, Italy (Seguenza, 1880) : *B. rosula*.
　　N. Italy, Sample SM 55, Torre Veglio Section (R. L. obs.) : *Batopora* sp.
　　Abruzzi, Italy (Ceretti & Poluzzi, 1970) : *B. multiradiata*.
　　Sardinia, Sample MU 214, Gesturi-Furtei, Central N. Campidano (R. L. obs.) :
　　　　Batopora sp.
　　Baden, near Vienna (Reuss, 1848) : *B. rosula*.
　　W. Aquitaine Basin (Le Saint, 1961) : *B. rosula* and *B. multiradiata*.
　　R.1103, Cuidad Granada Formation (*Globorotalia kugleri* zone), Velez Rubio,
　　　　T. B. Roep Coll. (R. L. obs.) : *B. rosula*.

MAP 1.   Distribution of species of *Batopora* in time and space (see Appendix 1).

OLIGOCENE.   Rockall Plateau, Site 117, 1038 m (Cheetham & Håkansson, 1972) :
  Batopora sp.
  Boring K 62, 23.90–24, 80 m surface, Ijzendijke, Netherlands (presumably
    Boom Clay, Rupelian) (R. L. obs.) : *B. asterizans* sp. nov.
  North Sea, Whitehall 43/3–1 well, 840–870 ft ditch cuttings (R. L. obs.) : *B.
    asterizans* sp. nov.
  Spain, Samples K 48–50, Moli de Llinares, Villajoyosa, Alicante Province
    (R. L. obs.) : *B. multiradiata.*
  Calbe and Saale, Germany (Reuss, 1867) : *B. stoliczkai.*

EOCENE.   Skalnik, Central Carpathians (Malecki, 1963) : *B. multiradiata* and *B.
    stoliczkai.*
  Buda, Marne de Buda (Couches à *Clavulinoides szaboi*) (Cook, 1966) : *B. multi-
    radiata.*
  Götzreuth, Bavaria (Koschinsky, 1885) : *B. scrobiculata* and *B. multiradiata*, and
    (P. L. C. obs.) USNM and BM : *B. grandis.*

Priabona and other northern Italian localities (Reuss, 1869 ; Waters, 1891 ; Braga, 1963) : *B. multiradiata*, *B. stoliczkai* and *B. rosula*.

Bordeaux area (Labracherie, 1961) : *B. stoliczkai*.

Sydenham and Hampstead, London Clay (Gregory, 1893) : *B. clithridiata*.

Appendix 2

The following records of *Lacrimula* and *Atactoporidra* have been plotted on Map 2.

RECENT.   Zanzibar, 101 and 207 m (Cook, 1966) : *L. burrowsi*, and *L. pyriformis*.

S.E. Africa, near Durban, 102 m (Cook, 1966) : *L. burrowsi*.

S. China Sea, 677 m (P. L. C. obs.) : *Lacrimula* sp.

HOLOCENE.   Bay of Bengal, E. India, 89 m (Rao & Rao, 1973) : *L. visakhensis*.

MIOCENE. Sample BG 312, Kombangan, Madura, Indonesia (N.E. Java) (R. L. obs.) : *L. similis* sp. nov., and *L. asymmetrica* sp. nov.

MAP 2.   Distribution of species of *Lacrimula* and *Atactoporidra* in time and space (see Appendix 2).

Sample G 5671, west of Batuputih, Madura, Indonesia (R. L. obs.) : *L. grunaui* sp. nov.

OLIGOCENE. North Sea, Whitehall 43/3–1 well, 840–870 ft ditch cuttings (R. L. obs.) : *L. borealis* sp. nov.

Belgium, Tongrian, Rupelian (Canu & Bassler, 1931) : *Atactoporidra bredaniana.*

EOCENE. Near Verona, and near Possagno, N. Italy (Accordi, 1947, and P. L. C. obs.) : *L. perfecta.*

Belgium, Wemmelian (Canu & Bassler, 1931) : *A. bredaniana.*

Selsey, Barton Clay, England (Cheetham, 1966) : *A. glandiformis.*

Marcheprime, Gironde (Labracherie, 1961) : *A. globosa.*

Appendix 3

The following records of *Conescharellina* have been noted. Those marked with an asterisk (*) are plotted on Map 3.

RECENT

Japan	*41°36′N, 140°36′E, no depth	(Canu & Bassler, 1929)	*C. catella*
	41°31′N, 140°36′E, 80·5 m		*C. parviporosa*
	*35°N, 139°E, 300 m	(Silén, 1947)	*C. striata*
	35°N, 131°E	(Harmer, 1957)	*C. catella*
	33°N, 129°E, no depth	(Silén, 1947)	*Conescharellina* spp.
	*33°05′N, 130°03′E, 40 m	(Silén, 1947)	*C. striata*
Hong Kong	*21°33′N, 116°15′E, 161 m	(Canu & Bassler, 1929)	*C. concava*
Philippines	13°21′N, 122°18′E, 970 m	(Canu & Bassler, 1929)	*C. breviconica*
	12°15′N, 123°57′E, 146 m	(Canu & Bassler, 1929)	*C. breviconica*
			C. milleporacea
			C. catella
	12°04′N, 124°04′E, 193 m	(Canu & Bassler, 1929)	*C. breviconica*
	11°09′N, 123°50′E, 60·5 m	(Canu & Bassler, 1929)	*C. milleporacea*
			C. breviconica
	*10°01′N, 124°42′E, 216 m	(Canu & Bassler, 1929)	*C. breviconica*
Celebes Sea	*6°44′N, 121°E, 46 m	(Canu & Bassler, 1929)	*C. jucunda*
			C. delicatula
			C. obliqua
	6°11′N, 121°08′E, 295·5 m	(Canu & Bassler, 1929)	*C. jucunda*
			C. delicatula
	6°09′N, 120°58′E, 53 m	(Canu & Bassler, 1929)	*C. milleporacea*
			C. elongata
	6°05′N, 121°02′E, 35 m	(Canu & Bassler, 1929)	*C. catella*
			C. grandiporosa
			C. elongata
	6°04′N, 120°58′E, 37 m	(Canu & Bassler, 1929)	*C. milleporacea*
			C. elongata
	5°41′N, 120°27′E, 44 m	(Canu & Bassler, 1929)	*C. milleporacea*
	5°41′N, 120°47′E, 38 m	(Canu & Bassler, 1929)	*C. lunata*
			C. elongata
	5°30′N, 120°07′E, 612 m	(Canu & Bassler, 1929)	*C. radiata*
	5°24′N, 120°27′E, 44 m	(Canu & Bassler, 1929)	*C. elongata*

RECENT (*cont.*)

Celebes Sea (*cont.*)	5°20′N, 119°58′E, 440 m 5°10′N, 119°47′E, 421 m	(Canu & Bassler, 1929) (Canu & Bassler, 1929)	*C. milleporacea* *C. elongata* *C. catella*
	4°54′N, 119°09′E, 310 m	(Canu & Bassler, 1929)	*C. radiata*
Malacca Str.	*4°20′N, 99°35′E, 50 m	(Silén, 1947)	*C. striata*
N. Celebes	1°N, 123°E, 72 m	(Harmer, 1957)	*C. elongata*
N. New Guinea	*0°, 130°E, 18–32 m	(Harmer, 1957)	*C. jucunda*
Makassar Straits & Java Sea	*1°19′S, 118°43′E, 2161 m	(Canu & Bassler, 1929)	*C. radiata* *C. transversa*
	2°S, 115°E, 59 m 2°30′S, 107°10′E, 15–27 m	(Harmer, 1957) (Silén, 1947)	*C. catella* *C. brevirostris* *C. longirostris* *C. laevis*
off Java	*7°S, 115°E, 88 m 7°S, 115°E, 1060 m	(Harmer, 1957) (Harmer, 1957)	*C. angustata* *C. distalis*
Java Sea	6°05′S, 114°07′E, 82 m	(Harmer, 1957)	*C. ovalis*
Arafura Sea	7°S, 132°E, 58·5–66 m	(BM)	*C. crassa*
Pt Moresby, Papua	*9°S, 147°E, no depth	(BM)	*C. crassa*
Torres Str.	9°, 140°E, 27·5–37 m	(BM)	*C. crassa*
Murray Is. Torres Str.	*10°S, 144°E, 27·5 m	(BM)	*C. conica*
Baudin Is. Timor Sea	12°S, 125′E, 27·5 m	(BM)	*Conescharellina* spp.
Holothuria Bank	*13°09′S, 126°22′E, 66–71 m 13°01′S, 125°58′E, 32 m	(BM) (BM)	*Conescharellina* spp. *Conescharellina* spp.
E. Australia	14°S, 144°E, 24 m (P. Charlotte Bay)	(Waters, 1921)	*C. philippinensis*
	19°42′S, 148°21′E, 42 m (Holborn Is.)	(Waters, 1921)	*C. conica*
	27°30′S, 152°30′E, no depth *32°30′S, 152°30′E, 40–46 m (Pt Stephens)	(Waters, 1921) (Waters, 1921)	*C. philippinensis* *C. cancellata* *C. philippinensis* *C. angulopora*
	33°S, 152°E, no depth 35 km E. of Pt Jackson, 146 m	(Waters, 1921) (BM)	*C. philippinensis* *C. biarmata* *C. angulopora* *C. eburnea*
S. E. Australia	36°S, 135°30′E, 190 m (56 km S.W. of Neptune Is.)	(BM)	*Conescharellina* sp.
	*40°S, 145°E, no depth (Bass Straits)	(Waters, 1921)	*C. angulopora*
S. E. Africa	*near Durban, 102 m	(Cook, 1966)	*C. africana*
E. Africa	*Zanzibar, 'Dalrymple' Stn 98, 69·5 m	(P. L. C. obs.)	*Conescharellina* sp.

PLIOCENE-PLEISTOCENE

S. Japan	*28°N, 130°E (Kikai Jima)	(Kataoka, 1961)	*Conescharellina* sp.
Sarawak	*3°35′N, 112°55′E (Patricia Is.)	(R. L. obs.)	*Conescharellina* sp.
Australia	*Weymouth Bore, Adelaide, 310–330 ft	(BM, P. L. C. obs.)	*Conescharellina* sp.

MIOCENE

Australia	*Bairnsdale, Gippsland and Curdies Creek	(Waters, 1887–9)	*C. cancellata* *C. philippinensis*
Indonesia	*G 5671, W. of Batuputih, Madura	(P. L. C. obs.)	*Conescharellina* sp.

MAP 3.   Distribution of species of *Conescharellina* and some problematical cone-
scharelliniform species in time and space (see Appendix 3).

EOCENE

Italy	*Mosciano, Italy	(Waters, 1921)	*C. eocoena* ?
Hungary	*Budapest	(Waters, 1921)	*C. eocoena* ?
France	*Landes, S. of Bordeaux	(Labracherie, 1970, 1971)	*Conescharellopsis vigneauxi* ?

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